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REVISION OF THE BEE GENUS AGAPOSTEMON (HYMENOPTERA: HALICTIDAE)

By

Radclyffe B. Roberts

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Revision of the Bee Genus *Agapostemon* (Hymenoptera: Halictidae)[1,2]

Radclyffe B. Roberts[3]

ABSTRACT

In this study 43 species of *Agapostemon* are recognized from the Americas. Of these, the following 19 species are new: *A. aenigma, A. alayoi, A. ascius, A. boliviensis, A. columbi, A. cubensis, A. cyaneus, A. erebus, A. hispaniolicus, A. inca, A. insularis, A. intermedius, A. jamaicensis, A. lanosus, A. mexicanus, A. mourei, A. ochromops, A. peninsularis, A. sapphirinus.* Forty-six names are listed as synonyms, 26 for the first time. Twenty-two species previously placed in *Agapostemon* but now placed in other genera are listed.

Separate keys are provided for species from America north of Mexico, Meso-America, The West Indies and South America. All species are described and most are illustrated. The geographic distribution and variation of the species and species groups are discussed, with particular regard to speciation of North American groups.

INTRODUCTION

The genus *Agapostemon* occurs only in the Western Hemisphere where it ranges from southern Canada to Paraguay. It is the only member of a group of allied genera to be found north of Mexico—South America being the center of abundance of most of its relatives.

Agapostemon is polythetic and cannot be differentiated from related genera on the basis of any one character or group of characters. Nevertheless, most species are characterized by their metallic green or blue head and mesosoma and their contrasting black or black and yellow metasoma.

Until recently, the biology of this genus was poorly known. However, in 1969 Eickwort and Eickwort described in detail the nesting and foraging behavior of *A. nasutus* in Central America. In the same year I reported on the biology of the North American *A. radiatus, A. splendens* and *A. texanus* and summarized available information on other species. These biological investigations have complemented the present classification.

The primary objective of this revision is to describe and classify the species of *Agapostemon* and to elucidate their evolutionary history. It is possible to recognize species groups and in some cases provide reasonable

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[2] This study was supported by National Science Foundation Grant GB 91 to the University of Kansas (C. D. Michener, principal investigator).

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explanations of their origins, but the number of species with no apparent affinities proscribes extensive speculation on the phylogeny of the genus.

A second objective of this work is to facilitate identification of species of *Agapostemon*. To this end keys, descriptions and illustrations have been prepared in as simple and uniform a style as possible. Species descriptions are in alphabetical sequence, because I believe a phenetic or "phylogenetic" sequence presumes too much knowledge on the part of the readers. The keys are regional and artificial for the sake of brevity and clarity respectively.

ACKNOWLEDGMENTS

I would like to express my gratitude to Dr. C. D. Michener for pointing out the need for this study; for examining specimens in Washington, London, Genoa, and in Pretoria, South Africa; and for his interest, encouragement, and guidance during the course of this study. Special thanks are also extended to Dr. G. W. Byers for his very helpful advice and careful editing of the manuscript.

The taxonomic portion of this study was made possible by the efforts of the curators, graduate students and others who selected and loaned nearly 50,000 specimens from the following collections: Academy of Natural Sciences of Philadelphia; American Museum of Natural History; Brigham Young University; British Museum (Natural History); California Department of Agriculture (Sacramento); Canadian National Collection; Carnegie Museum; Chicago Natural History Museum; Colorado State University; Cornell University; Florida State Collection of Arthropods, Gainesville; Illinois Natural History Survey; Iowa State University; Instituto e Museo di Zoologia Universita di Torino; Kansas State University; Los Angeles County Museum; Michigan State University; Milwaukee Public Museum; Montana State College; Museo Civico di Storia Naturale (Genoa); Muséum National d'Histoire Naturelle (Paris); Museum of Comparative Zoology; Naturhistorisches Museum (Vienna); North Carolina State of the University of North Carolina; Northwestern State College (Louisiana); Ohio State University; Oklahoma State University; Oregon State University; Pennsylvania State University; Purdue University; Riksmuseum van Natuurlijke Historie (Amsterdam); Rutgers, The State University; San Jose State College; South Dakota State College; Stanford University; Transvaal Museum (Pretoria, South Africa); United States Department of Agriculture, Wild Bee Pollination Investigations (Logan, Utah); United States National Museum; University of Arizona; University of Arkansas; University of California at Berkeley, Davis, and Riverside; University of Colorado; University of Georgia; University of Idaho; University of Kansas; University of Louisville (Kentucky); University of Michigan; University of Minnesota; University of Missouri; University of Nebraska; University of Nevada; University of North Dakota; University of Tennessee; University of Wisconsin; University of Wyoming; Utah State University; Washington State University; Zoologisches Museum der Humboldt-Universität (Berlin).

The following individuals graciously loaned specimens from their personal collections: Pastor Alayo D., Havana, Cuba; the late R. R. Dreisbach (collection

now at Michigan State University); R. A. Morse, Cornell University; D. W. Ribble, University of Wyoming; and G. I. Stage, United States National Museum. Through their cooperation and hospitality the following individuals did much to make my visits to museums both profitable and pleasant: P. H. Arnaud, Jr., California Academy of Sciences; G. E. Bohart, U.S.D.A., Logan, Utah; K. V. Krombein and G. I. Stage, U.S. National Museum; J. G. Rozen, Jr., American Museum of Natural History; the late J. A. G. Rehn and the late H. J. Grant, Academy of Natural Sciences of Philadelphia.

Finally, I am grateful to my wife, Guinnevere, whose multifarious talents as collector, observer, secretary, editor and counselor have contributed immeasurably to the completion of this study.

HISTORICAL REVIEW

The taxon *Agapostemon* was first proposed in 1844 by F. E. Guérin-Méneville as a subgenus of *Andrena* in the following statements:

> Nous connaissons plusieurs espèces à cuisses ainsi renflées. Ce sont des mâles. Peut-être jugera-t-on à propos de les réunir en un sous-genre, que nous proposerions de nommer *Agapostemon*. Il serait aux Andrenes ce qu'est le genre *Nomia* parmi les Halictes.

The only included species was *Andrena (Agapostemon) femoralis* Guérin 1844. Dalla Torre (1896) correctly recognized this species to be a junior synonym of *Apis viridula* Fabricius 1793. Therefore the correct name for the type species of the genus *Agapostemon* is now *Agapostemon viridulus* (Fabricius). *Agapostemon* was first described and accorded generic rank in 1853 by Frederick Smith, who listed seven species, four of them new. In 1896 Dalla Torre catalogued 16 species and placed four species in synonymy. He also gave the Latin translation of Guérin's transliterated Greek compound, *Agapostemon*, as "*αγαπαω amo, στημων stemen*." In English the translation is "lover of stamens."

In 1897 Robertson redescribed the species known from the United States and listed their synonyms. The first key, published by Titus in 1901, included only the species known to occur in Colorado, and in November of the same year Crawford revised the North American species of *Agapostemon*. In this revision Crawford re-described the genus, described seven new species, and included a key to the 15 species then known from North America. In 1902 Robertson published keys to the genera and species of the North American Halictinae in which he commented on the relationships of the genera. Although he cited very few characters, the keys and generic concepts were remarkably good.

In 1903 Vachal reduced *Agapostemon* to subgeneric rank in *Halictus*. He included 28 species (nine of them new) in the subgenus *Agapostemon* and proposed the new subgenus *Paragapostemon* for 25 additional species

with hairy eyes and without a complete propodeal carina. Although his keys were good, Vachal's conservative generic concepts were not widely accepted, and Cockerell (1905) accorded generic rank to both *Agapostemon* and *Paragapostemon*. Vachal did not cite a type species for *Paragapostemon*, but Cockerell (1905, in footnote) designated *Halictus (Paragapostemon) podager* Vachal as the type species.

Schrottky (1909a) erected the genus *Pseudagapostemon* (type species *Agapostemon arenarius* Schrottky), thereby removing most of the species from *Paragapostemon* as well as additional species from *Agapostemon*. Schrottky published another paper (1909b) in which he reduced seven species of South American *Agapostemon* to synonymy and transferred four more from *Agapostemon* to *Pseudagapostemon*. In 1918(a) Cockerell reduced *Pseudagapostemon* to subgeneric rank in *Agapostemon*, but never referred to it as such thereafter.

In 1936 Sandhouse revised the species of *Agapostemon* occurring in the United States. Although she examined about 4,000 specimens, her work does not make sufficient allowance for intraspecific variation, none of the species are described, the only figures (of genitalia) are inadequate, and finally, she did not recognize five of the species now known from the United States; *A. femoratus, A. tyleri, A. nasutus, A. peninsularis* and *A. leunculus*. Despite these shortcomings, Sandhouse's revision has remained the best available reference on the genus for more than thirty years. More recent systematic treatments of *Agapostemon* are the contribution by Michener (1951) to the catalog of North American Hymenoptera; and the key, descriptions and figures for the species in the eastern United States (Mitchell, 1960).

EXCLUDED SPECIES

The following is a list of species which, although described in or subsequently transferred to *Agapostemon*, are no longer considered to belong to this genus. When possible the genus to which they belong has been indicated. Some of the species are synonyms but listing of synonymies must be postponed until *Paragapostemon* and *Pseudagapostemon* can be revised.

In 1918(a) Cockerell reduced *Pseudagapostemon* to a subgenus of *Agapostemon* but this classification has never won acceptance. The only species mentioned by Cockerell [*Agapostemon (Pseudagapostemon) xanthorhinus* Cockerell, *Halictus citricornis* Vachal, *Pseudagapostemon paulista* Schrottky, and *Pseudagapostemon nasua* Schrottky] have been omitted from the following list.

Augochloropsis

Agapostemon caeruleus Ashmead 1890 was placed in *Augochloropsis* by Titus (1901).

Paragapostemon

Nomia caelestina Westwood 1875, placed in *Agapostemon* by Cockerell (1910a), was placed in *Paragapostemon* by Moure (1964).

Agapostemon bruneri Crawford 1901 was placed in *Paragapostemon* by Moure (1964).

Halictus (Agapostemon) sicheli Vachal 1901 was placed in *Paragapostemon* by Moure (1964).

Nomia tacita Cameron 1902, placed in *Agapostemon* by Cockerell (1910a), was placed in *Paragapostemon* by Moure (1964).

Nomia cillaba Cameron 1902, placed in *Agapostemon* by Cockerell (1910a), was placed in *Paragapostemon* by Moure (1964).

Ruizantheda

Halictus emarginatus Spinola 1851, placed in *Agapostemon* by Cockerell (1905), is a synonym of the type species (*Halictus proximus* Spinola 1851) of *Ruizantheda* Moure 1964.

Halictus mutabilis Spinola 1851, placed in *Agapostemon* by Schrottky (1903), became the type species of *Ruizantheda (Ruizanthedella)* Moure 1964.

Halictus placidus Smith 1879 was placed in *Agapostemon* by Cockerell (1905), but Moure *(in litt.)* places it in *Ruizantheda.*

Pseudagapostemon

Agapostemon arenarius Schrottky 1902(b) became the type species of *Pseudagapostemon* Schrottky 1909(a).

Agapostemon aeneus Schrottky 1902(a) was placed in *Pseudagapostemon* by Schrottky (1909b).

Agapostemon arechavaletae Schrottky 1908 was placed in *Pseudagapostemon* by Schrottky (1909b).

Agapostemon bonaërensis Schrottky 1908 was placed in *Pseudagapostemon* by Schrottky (1909b).

Halictus (Agapostemon) pissisi Vachal 1903 was placed in *Pseudagapostemon* by Vachal (1904).

Halictus (Agapostemon) divaricatus Vachal 1903 was placed in *Pseudagapostemon* by Vachal (1904).

Agapostemon olivaceo-splendens Strand 1910 was placed in *Pseudagapostemon* by Moure (1947).

Agapostemon zosteronedys Moure 1940 belongs in *Pseudagapostemon divaricatus* (Vachal) as indicated by Moure (footnote in Michener and Lange, 1958).

Species *Incertae Sedis*

Halictus bruchianus Schrottky 1908 was placed in *Agapostemon* by Schrottky (1913). Moure *(in litt.)* has not seen the type but believes it should be placed in *Corynura* or *Ruizantheda* (probably the latter).

GENERIC DIAGNOSIS

No one character or set of characters was found to be both necessary and sufficient to distinguish all species of *Agapostemon* from all species in other halictine genera. However, the genus may be recognized by a syndrome of characters. This set of characters is common to most species of *Agapostemon* but not all of its characters are present in all of the species.

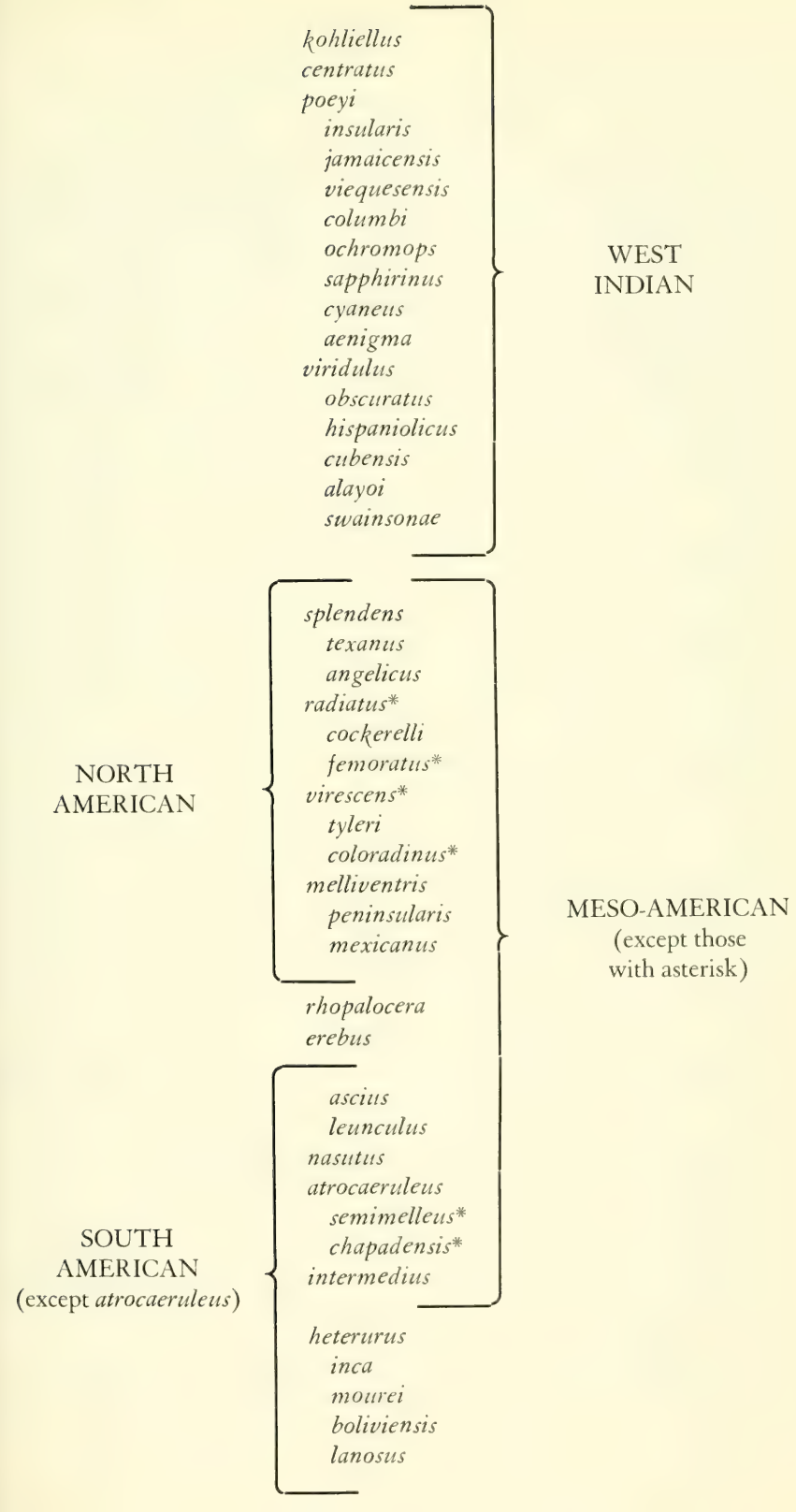
The character which is unique to *Agapostemon* and which best separates this genus from other halictine genera is the carina which in most species entirely surrounds the posterior surface of the propodeum of both sexes. Also unique among halictines is the striking contrast between the non-metallic coloration of the metasoma and the metallic coloration of the head and mesosoma of most female and nearly all male *Agapostemon*.

Female *Agapostemon* may be distinguished from females of most other halictine genera by the three or four (sometimes as many as seven) large spatulate teeth on the posterior hind tibial spur and by the parallel contiguous carinae extending postero-dorsally from the antero-ventral margin of the gena. Male *Agapostemon* may be distinguished from males of the augochlorine genera and the genera in the *Halictus-Lasioglossum* group by the fusion of the first two tarsomeres of the hind tarsus. Unlike those of almost all other halictine genera, the hind femora and, to a lesser extent, the hind tibiae of many male *Agapostemon* are conspicuously swollen. The only other genera with similarly modified legs have conspicuously hairy eyes in contrast to the glabrous or nearly glabrous eyes of *Agapostemon*.

INFRAGENERIC STRUCTURE

While it seems premature to speculate at length on the phylogeny of the species of *Agapostemon*, certain discrete groups of species can be recognized on the basis of such features as genitalia, pronotum, legs, metasomal sterna and color pattern. These species groups might have been recognized as subgenera, but to be consistent I would have been forced to recognize an unacceptable number of small or monotypic subgenera. Subspecies are not recognized because there is little biological or utilitarian justification for such in this genus. Of course, intra-specific variation is described wherever encountered.

In the following list the name of the first member (chosen arbitrarily) of each species group has not been indented and will serve to identify the group in subsequent discussion (e.g., the species in the *splendens* group are *A. splendens, A. texanus* and *A. angelicus*).


kohliellus
centratus
poeyi
insularis
jamaicensis
viequesensis
columbi
ochromops
sapphirinus
cyaneus
aenigma
viridulus
obscuratus
hispaniolicus
cubensis
alayoi
swainsonae
WEST INDIAN
splendens
texanus
angelicus
radiatus*
cockerelli
femoratus*
virescens*
tyleri
coloradinus*
melliventris
peninsularis
mexicanus
NORTH AMERICAN
MESO-AMERICAN (except those with asterisk)
rhopalocera
erebus
ascius
leunculus
nasutus
atrocaeruleus
semimelleus*
chapadensis*
intermedius
SOUTH AMERICAN (except atrocaeruleus)
heterurus
inca
mourei
boliviensis
lanosus

ZOOGEOGRAPHY

Although more than 50,000 specimens were examined in the course of this study, I was hampered by inadequate collections from the West Indies as well as Central and South America. While it seems unlikely that any new North American species will be discovered, it is likely that new species remain to be found in the West Indies, Central America and the Andean region of South America.

It is difficult to comprehend what factors influence the distribution of species of *Agapostemon*. Only in the correlation between the distribution of *A. splendens* and that of moist sandy soils in the eastern United States and eastern Mexico is there evidence of a causal relation between the presence of an ecological parameter and the presence of the bees (Roberts, 1969).

Some species, such as *A. coloradinus,* are relatively restricted in range while others are widespread, *A. texanus* occurring from Canada to Costa Rica and Boston to San Francisco. In the United States alone, *A. texanus* occurs in 70 of 116 plant communities (Appendix A). *A. angelicus* occurs from below sea level in Death Valley, California to 12,000 ft. (3,658 m) on Mt. Evans in Colorado (timberline 11,700 ft.). In view of the apparent ecological plasticity among most species, it is not surprising that their distributions broadly overlap.

North American Species. There are four North American species groups. Each of these groups is composed of two very similar species and a third species which, although obviously closely related, stands somewhat apart phenetically. In each group but one, the two most similar species are found west of the 95th meridian and the third species is found north and east of the others. There is some sympatry within each species group, but the center of distribution is different for each species within a group (Fig. 228).

The simplest explanation for the occurrence of these similar geographic and cladistic patterns in each of the North American species groups is to assume: (1) North America was originally occupied by four species; (2) each species was bisected into southeastern and southwestern populations at the time of Pleistocene glaciation; and (3) the southwestern populations were more recently subdivided (possibly on the Pacific and Gulf coasts of Mexico) when forced to migrate farther south by still further cooling. Presumably this pattern of evolution is not evident among the Meso-American and West Indian species groups because they were too far south to have been significantly displaced by the climatic changes accompanying Pleistocene glaciation.

West Indian Species. The West Indian species are interesting in that they are not found on the mainland (with the doubtful exception of *A.*

aenigma) and are not closely related to the mainland species. This is somewhat surprising in view of their relative proximity to the Florida and Yucatan peninsulas. Also surprising is their absence in the lesser Antilles; yet their occurrence throughout the Bahama Islands and Greater Antilles constitutes prima-facie evidence of high vagility.

Although it is extremely improbable that the bees fly of their own accord between islands, it does seem likely that they are occasionally swept up by hurricanes and deposited on other islands many miles distant. Members of the *poeyi* and *viridulus* groups are widespread (cf. map, Fig. 1). As there is very little discernible correlation of geographic factors with the phenotype among members of each of these phenetically homogeneous species groups, I am inclined to believe that, relative to their rates of evolution, their rates of dispersal have been rapid.

In studying the *poeyi* group I vacillated between considering all of the island populations as conspecific and considering each population as a separate species. *A. poeyi* and *A. viequesensis,* occurring in Cuba and Puerto Rico respectively, have long been considered as distinct species which could easily be differentiated morphologically. However, as morphologically intermediate forms exist on the Bahama Islands, it is tempting to classify the entire group as a single highly variable species. However, phenetically typical populations of *A. poeyi* and *A. viequesensis* are sympatric on New Providence Island, and there is no evidence of hybridization. The phenetic homogeneity within each of the phenetically different populations of this complex on other islands leads me to believe that gene flow between these allopatric populations is also inconsequential. Thus it seems that in the *poeyi* group the rate of speciation, or creation of clades, is high relative to the rate of evolution, or shift in gene frequency. Although not as large and widespread, the *viridulus* group similarly appears to be speciating relatively rapidly. My decision to regard the *A. poeyi* group as an *Artenkreis* rather than a *Rassenkreis* is based on scanty evidence. However, the decision is a taxonomic necessity which in no way effects the biological attributes of the organisms in question.

The species *A. kohliellus* and *A. centratus* do not seem closely related to any other species of *Agapostemon*. Rare species, they may be restricted to a particular ecological factor found only on the island of Hispaniola. Such a severe ecological limitation could explain their absence on the other islands.

Meso-American Species. The distributions and relationships of the species occurring in this region are difficult to interpret. Some of the species such as *A. mexicanus* or *A. tyleri* clearly belong to North American groups although *A. mexicanus* is found in northwestern Mexico and *A. tyleri* ranges southward on the central plateau to the vicinity of Mexico City.

A. rhopalocera is a rare species known only from males, not obviously

related to other species and restricted to the vicinity of Mount Orizaba in Vera Cruz. *A. erebus* is known from a single female collected in El Salvador, but is obviously closely related to *A. leunculus* which ranges from the southern tip of Texas to eastern Ecuador, and also to a third species, *A. ascius,* known from two females collected in Colombia.

Males of *A. nasutus* are unlike those of any other species inasmuch as their genitalia and clypeal region are both highly modified. They also differ from males of other species in less striking features such as the lateral tufts of pubescence on the 6th metasomal sternum. Despite these obvious peculiarities of males, females of *A. nasutus* are somewhat similar to those of the *erebus* group (differing principally in the shape of the pronotum). The commonest species throughout most of its range, *A. nasutus* is found from the southern tip of Texas to northern South America, as far east as Trinidad, and west of the Andes as far south as Ica, Perú.

A. atrocaeruleus has been found only in Costa Rica but is closely related to a pair of species found primarily south of the Amazon Basin but reaching as far north as Ecuador. *A. intermedius* is found from Costa Rica to Tingo Maria, Perú and obviously links the *atrocaeruleus* group with the Andean *heterurus* group.

In summary, most of the Meso-American species of *Agapostemon* belong in North or South American species groups. Only the very widespread and abundant *A. nasutus* and the very restricted and rare *A. rhopalocera* have no apparent affinities with either North or South American species, or each other.

South American Species. Some of the species occurring in South America such as *A. nasutus, A. intermedius* and *A. ascius* are restricted to the northwestern margin of the continent. Apparently these species, which are recently evolved or recently arrived via Central America (e.g., *A. nasutus*), have found further access to the continent blocked by the Andes to the east, the Atacama Desert to the south, and the forests of the Orinoco Basin to the north.

Agapostemon chapadensis and *A. semimelleus* are the only species widely distributed in South America. Both are found in the *campos,* or subtropical grasslands, of southern Brasil, Paraguay and northern Argentina. In addition isolated populations of *A. semimelleus* have been collected from the headwaters of the Marañon, Huallaga and Cauca rivers. Presumably, these species were able to ascend the valleys at some time in the past when the South American grasslands were more extensive than today. Surprisingly, *A. semimelleus* has been collected at the head of the Cauca Valley in Colombia. I cannot explain this occurrence as the Cauca River drains into the Caribbean Sea. Specimens of *A. semimelleus* have been collected from localities as near as the headwaters of the Putumayo River, but the Cauca and Putumayo

rivers are separated by at least 200 kilometers of mountains (Cordillera Central) rising as high as 5755 m. The closest relative of *A. semimelleus* and *A. chapadensis* is *A. atrocaeruleus* which has been collected only on the central plateau of Costa Rica, nearly 1000 km from the headwaters of the Cauca River.

The most aberrant species group in *Agapostemon* includes *A. heterurus, A. inca, A. boliviensis, A. lanosus* and *A. mourei.* These species are very closely related and are restricted to the eastern margins of the central Andes. As many of the valleys in this region are both ecologically isolated and poorly collected, it seems reasonable to predict that more species in this group will be discovered.

A. intermedius is morphologically intermediate between the *A. heterurus* group and the *A. atrocaeruleus* group. *A. intermedius* ranges from central Costa Rica, where it is sympatric with *A. atrocaeruleus,* to northwestern South America. It has also been collected from Tingo Maria at the head of the Huallaga Valley where it is sympatric with *A. lanosus.* Possibly *A. intermedius* is part of an *Artenkreis* running from Costa Rica down to the grasslands of Brasil (the *A. atrocaeruleus* group) and down to the eastern margins of the Andes (the *A. heterurus* group).

METHODS

Terminology. The terminology is essentially that utilized by Michener (1944, 1965). However, the following terms have been proposed since no appropriate ones existed for these features.

The *propodeal shield* is the flat or slightly concave area on the posterior vertical surface of the propodeum usually delimited by a conspicuous *propodeal carina* (Fig. 25). Male genitalia often bear an *apical stylus, medial plate* and *basal stylus* on the mesal surface of the gonostylus (Fig. 180). Although often reduced and covered by long bristles, a *ventral lobe* (Fig. 223) is always present on the ventral surface of the gonocoxite.

The specific importance of the maculations of male legs has necessitated a more precise and morphologically consistent system for designating various portions of the legs than that used by Michener and others. The legs of bees, like those of most insects, may move anteriorly and posteriorly, and may be flexed ventrally and extended laterally. The middle legs, when extended, are nearly perpendicular to the longitudinal axis of the body (presumably the "primitive" condition in the Arthropoda). The fore legs and hind legs, however, are directed respectively forward and rearward to a greater or lesser degree. Owing to the rearward orientation of the hind legs of bees (especially in pinned specimens and in live bees in flight), that which is designated by previous authors as the "inner" surface of the hind legs is not homologous with what they term the "inner" surface of the fore legs.

Therefore, I propose a terminology consistent with the presumed serial homology of the parts of the three pairs of legs rather than with the positions in which they are borne. Although this system may at first seem strange and cumbersome, it is economical in that one can refer, for example, to serially homologous maculations as being on the posterior surfaces of all three pairs of legs. With the system used by other authors one could not refer to such maculations as being on the "inner" surfaces of all three pairs of legs. The disadvantage of the proposed system is that the "dorsal" quadrant of the tarsus may be visible only from below (due to the flexed position of the leg), and the "anterior" surface of the hind leg only from the side.

In the following descriptions, the legs are considered as extended at right angles to a sagittal plane through the body of the bee. The hypothetical leg segment is regarded as cylindrical, its cross-section divided by perpendicular diagonals into dorsal, ventral, anterior and posterior quadrants.

DESCRIPTION. To conserve space, the reader is often referred to the description of another species or sometimes the opposite sex. All interspecific comparisons are between members of the same sex unless otherwise specified.

Because sexual dimorphism is so pronounced in *Agapostemon*, characters used to differentiate males (or females) of two closely related species are not always present on members of the opposite sex. In some instances members of only one sex can be differentiated morphologically. In other cases the morphological differences between species are so subtle as to render identification difficult regardless of sex. For these reasons distributions have been used (especially in the keys) wherever morphological differentiation was difficult or impossible. Of course, no species is recognized solely on the basis of its distribution. The reader must be cautious in relying on distributional differentia because the ranges of species are subject to change without notice.

If two species are very similar then only one is described and the other is described as identical but for the differentiating characters. Relative size is presented as proportions and absolute size may be derived from scale drawings. For each character, the drawings are to the same scale to facilitate size comparisons between species.

Synonymies have been kept as brief as possible and no references to synonyms have been made unless they involve nomenclatural changes of specific epithets. An effort was made to locate and examine the primary types of all nominal species and subspecies and, whenever possible, their location has been noted in the synonymy. In quotations of label data on the types of new species, a single slash indicates the break between lines on a label and a double slash the break between labels on a pin.

KEY TO SPECIES OF THE UNITED STATES AND CANADA

1. Female; 10 flagellomeres; scopa on hind leg 2
Male; 11 flagellomeres; scopa absent 14

2.(1) Metasomal terga bright metallic green to blue, concolorous with head and mesosoma 3
Metasomal terga black to pale amber, not concolorous with metallic head and mesosoma 7

3.(2) Wings almost hyaline, only slightly darkened on distal margins; mandible yellow basally 4
Wings transparent brown, distal margins conspicuously darkened; mandible usually amber basally (rarely yellow) ..... *splendens*

4.(3) Mesoscutum with numerous fine punctures interspersed with fewer distinctly larger and deeper punctures; punctuation often so fine as to leave mesoscutum shiny (Figs. 23, 24) ..... *texanus* and *angelicus**
Mesoscutum coarsely punctate or rugose, lacking punctures of two distinct sizes and never shiny 5

5.(4) Mesoscutum coarsely rugose at least on inner borders of parapsidal lines, if not rugose throughout ..... *femoratus*
Mesoscutum between parapsidal lines coarsely punctate, not rugose 6

6.(5) Common in eastern half of U.S., becoming rare in the Great Plains (Fig. 18) ..... *radiatus*
Common on Mexican Plateau and in arid southwestern U.S., rare along eastern border of Rocky Mountains (Fig. 2) ..... *cockerelli*

7.(2) Posterior lobe of pronotum with pale yellow or creamy spot at apex (Fig. 134); clypeus with yellow transverse band (Fig. 42) ..... *nasutus*
Posterior lobe of pronotum metallic at apex, never creamy or yellow; clypeus with or without yellow transverse band 8

8.(7) Clypeus with transverse apical or subapical yellow band; metasoma black or pale amber 9
Clypeus metallic with apical region dark brown to black; metasoma always black 10

9.(8) Pronotum with single conspicuous sharp carina extending postero-ventrally from lateral angle (Fig. 135); metasomal terga black with narrow basal bands of white tomentum; scape dark brown to black, lacking yellow ..... *leunculus*
Pronotum without conspicuous sharp carina extending postero-ventrally from lateral angle (may have several small carinulae); metasomal terga pale amber to black, with white tomentum on basal halves; scape sometimes marked with yellow 12

10.(8) Genal ridges coarse (2-3 per 0.25 mm) (Fig. 28); mandible usually yellow basally ..... *virescens*
Genal ridges fine (5-6 per 0.25 mm); mandible amber to brown-black basally 11

* The females of *A. texanus* and *A. angelicus* cannot be reliably separated on the basis of their morphology; however, females occurring well outside the range of *A. angelicus* males are probably *A. texanus* (see map, Fig. 20).

11.(10) Wings transparent brown; white tomentum lacking on anterior part of first metasomal tergum; protuberance above clypeus without large, central, shiny area ..... *coloradinus*
Wings hyaline, not brown; white tomentum on anterior part of first metasomal tergum 13

12.(9) Dorsal area of propodeum moderately to coarsely rugose; scape often marked with yellow; metasomal terga amber to black or black with amber anteriorly on tergum 1 ..... *melliventris*
Dorsal area of propodeum finely rugose to finely rugulose; scape never with yellow markings; metasomal terga always entirely black ..... *peninsularis*

13.(11) Supraclypeal protuberance with smooth shiny central area with scattered punctures; found only in Arizona, New Mexico and on the Mexican Plateau (Fig. 27) ..... *tyleri*
Supraclypeal protuberance with weakly and transversely rugose central area; occurs around Gulf of California ..... *mexicanus***

14.(1) Clypeus conspicuously concave ventrally, more than three times as broad as long (Figs. 86, 87) ..... *nasutus*
Clypeus normal, little broader than long 15

15.(14) First metasomal tergum yellow to very pale amber basally, not brown or black, and hind basitarsus always slender and simple (Fig. 155); hind leg yellow with small brown or black area apically on femur and basally on tibia ..... *melliventris*
First metasomal tergum brown to black basally (if pale amber, then hind basitarsus swollen and with basal ridge and apical groove); hind leg usually with dark brown to black stripe on tibia 16

16.(15) Hind femur without tooth; slender 25
Hind femur with subapical tooth postero-ventrally; often conspicuously inflated 17

17.(16) Wings transparent brown, conspicuously darkened at distal margins; hind basitarsus with crest of basal ridge grooved (Fig. 166) ..... *splendens*
Wings hyaline or nearly so, not conspicuously darkened at distal margins; hind basitarsus with basal ridge (if present) not grooved 18

18.(17) Metasoma with last two visible sterna (5-6) dark brown to brown-black, without yellow maculations; sterna 2-4 with yellow (if present) restricted to basal margins 19
Metasoma with extensive yellow maculations on last two visible sterna (5-6) as well as on sterna 2-4 21

19.(18) Hind femur lacking brown to black stripe on posterior surface (Fig. 158) ..... *virescens*
Hind femur with large brown to black stripe covering most or all of posterior surface 20

20.(19) Brown to black streak less than ⅔ length of posterior surface of hind tibia (Fig. 160) ..... *coloradinus*
Brown to black streak extending entire length of posterior surface of hind tibia (Fig. 159) ..... *tyleri*

** Although not currently known to occur in the United States, this species may yet be found in the vicinity of San Diego or Yuma, thus it is included in this key.

21.(18) Metasomal sternum 4 (antepenultimate visible) with low transverse ridge not quite reaching posterior margin laterally; metasomal tergum 4 usually without conspicuous metallic tints 22
Metasomal sternum 4 (antepenultimate visible) with low transverse ridge reaching posterior margin laterally; metasomal tergum 4 nearly always with conspicuous metallic tints 24

22.(21) Hind basitarsus lacking apical groove and basal ridge (Fig. 161) ..... *radiatus*
Hind basitarsus with apical groove and basal ridge 23

23.(22) Hind basitarsus with inconspicuous basal ridge and slender apical groove (Fig. 162) ..... *cockerelli*
Hind basitarsus with very large, conspicuous, slightly sinuate basal ridge and broad, conspicuous apical groove (Fig. 163) .... *femoratus*

24.(21) Base of apical stylus of gonostylus slightly inflated (Fig. 181); brown to black stripe on posterior surface of hind tibia but never on anterior surface (Fig. 164) ..... *angelicus*
Base of apical stylus of gonostylus not inflated (Fig. 180); brown to black stripe anteriorly on hind tibia (Fig. 165), or, if lacking, then without black stripe on posterior surface ..... *texanus*

25.(16) Posterior surface of hind tibia largely yellow (Fig. 143) ..... *leunculus*
Posterior surface of hind tibia largely brown or black 26

26.(25) 2-4 large submarginal bristles on each side of metasomal sternum 4 ..... *peninsularis*
14-20 large, evenly spaced submarginal bristles on metasomal sternum 4 ..... *mexicanus**

KEY TO MESO-AMERICAN** SPECIES

1. Males; 11 flagellomeres; scopa absent 2
Females; 10 flagellomeres; scopa on hind legs 15

2.(1) Antenna normal 3
Antenna long, filamentous, and with apical flagellomere flattened (Fig. 131) ..... *rhopalocera*

3.(2) Clypeus normal, little longer than broad 4
Clypeus conspicuously concave ventrally, more than three times as broad as long (Figs. 86, 87) ..... *nasutus*

4.(3) Metasoma banded with yellow and dark brown or black, lacking bands of white tomentum 5
Metasoma pale amber, with bands of white tomentum ..... *centratus*

5.(4) Sixth metasomal sternum flat or with inconspicuous medial ridge 6
Sixth metasomal sternum with medial "button" (flattened process resembling human tongue and attached to sternum in much the same way as human tongue is attached to floor of mouth (Fig. 136) ..... *intermedius*

6.(5) Hind femur with conspicuous subapical tooth postero-ventrally 7
Hind femur lacking tooth 11

* Although not currently known to occur in the United States, this species may yet be found in the vicinity of San Diego or Yuma, thus it is included in this key.

** Mexico, Panama, and intervening countries.

7.(6) Wings hyaline or nearly so, not conspicuously darkened at distal margins; hind basitarsus with basal ridge (if present) not grooved 8
Wings transparent brown, conspicuously darkened at distal margins; hind basitarsus with crest of basal ridge grooved (Fig. 166) ..... *splendens*

8.(7) Metasoma with extensive yellow maculations on sterna; hind tibia with brown or black posterior stripe (when present) not extending from base to apex 9
Metasoma with sterna brown or black, lacking yellow maculations; hind tibia with broad brown or black posterior stripe extending from base to apex ..... *tyleri*

9.(8) Metasomal sternum 4 (antepenultimate visible) with low transverse ridge reaching posterior margin laterally; metasomal tergum 4 nearly always with conspicuous metallic tints 10
Metasomal sternum 4 (antepenultimate visible) with low transverse ridge not quite reaching posterior margin laterally; metasomal tergum 4 without conspicuous metallic tints ..... *cockerelli*

10.(9) Base of apical stylus of gonostylus slightly inflated (Fig. 181); brown to black stripe on posterior surface of hind tibia but never on anterior surface (Fig. 164) ..... *angelicus*
Base of apical stylus of gonostylus not inflated (Fig. 180); brown to black stripe anteriorly on hind tibia (Fig. 165) or, if lacking, then without black stripe on posterior surface ..... *texanus*

11.(6) Base of metasomal tergum 1 dark brown or black 12
Base of metasomal tergum 1 yellow or pale amber ..... *melliventris*

12.(11) Hind leg with broad brown or black stripe covering most of posterior surface of tibia and extending from base to apex; similar stripe on femur sometimes broken centrally 13
Hind leg largely yellow on posterior surface of tibia and femur 14

13.(12) Metasomal sternum 4 with 2-4 large submarginal bristles on each side ..... *peninsularis*
Metasomal sternum 4 with 14-16 large, evenly spaced submarginal bristles ..... *mexicanus*

14.(12) Pronotum with very acute lateral angle; mesoscutum with conspicuous flange laterally on anterior margin ..... *atrocaeruleus*
Pronotum with lateral angle rounded; mesoscutum lacking flange on anterior margin ..... *leunculus*

15.(1) Metasomal terga bright metallic green to blue-green 16
Metasomal terga pale amber to black, not metallic 19

16.(15) Mandibles amber with metallic green spot basally; dorsal area of pronotum with very large, widely separated carinae extending from anterior margin to propodeal carina ..... *aenigma**
Mandibles amber or yellow, lacking metallic spot basally; pronotum rugose dorsally 17

17.(16) Wings almost hyaline, only slightly darkened on distal margins; mandibles yellow basally 18
Wings transparent brown, distal margins conspicuously darkened; mandibles usually amber (sometimes yellow) basally .... *splendens*

* Although labeled "Costa Rica" the two specimens of *A. aenigma* are closely related to West Indian species and may be mislabeled.

18.(17) Mesoscutum coarsely punctate to finely rugose, lacking punctures of two distinct sizes and never shiny ..... *cockerelli*
Mesoscutum with numerous fine punctures interspersed with fewer distinctly larger and deeper punctures, punctation often so fine as to leave mesoscutum shiny (Figs. 23, 24) .... *texanus* and *angelicus***

19.(15) Lateral angle of pronotum acutely pointed; mesoscutum with conspicuous flange laterally on anterior margin 20
Lateral angle rounded, not acutely pointed; mesoscutum lacking conspicuous flange on anterior margin 21

20.(19) Head and mesosoma black (usually with inconspicuous dark blue tints and with yellow band on clypeus); metasoma black with bands of white tomentum ..... *atrocaeruleus*
Head and mesosoma metallic green or coppery; metasoma pale amber to black, with yellow integumental bands replacing usual bands of white tomentum ..... *intermedius*

21.(19) Posterior lobe of pronotum metallic at apex, never creamy or yellow; clypeus with or without yellow transverse band 22
Posterior lobe of pronotum with creamy or yellow spot at apex; clypeus with yellow transverse band ..... *nasutus*

22.(21) Clypeus with transverse, subapical, yellow band; metasoma amber to black 23
Clypeus black at apical margin, lacking yellow band; metasoma always black 25

23.(22) Pronotum without single conspicuous sharp carina extending postero-ventrally from lateral angle (may have several small carinulae); metasomal terga pale amber to black, with white tomentum on basal halves; scape dark brown to black, sometimes marked with yellow 24
Pronotum with single conspicuous sharp carina extending postero-ventrally from lateral angle; metasomal terga with narrow basal bands of white tomentum; scape dark brown to black, lacking yellow ..... *leunculus*

24.(23) Dorsal area of propodeum moderately to coarsely rugose; scape often marked with yellow; metasomal terga amber to black, or black with amber anteriorly on tergum 1 ..... *melliventris*
Dorsal area of propodeum finely rugose to finely rugulose; scape never with yellow markings; metasomal terga always entirely black ..... *peninsularis*

25.(22) Head and mesosoma bright metallic green 26
Head and mesosoma black with metallic purple tints ..... *erebus*

26.(25) Supraclypeal protuberance with smooth shiny central area and with scattered punctures; occurs in New Mexico, Arizona, and on the Mexican Plateau (Fig. 27) ..... *tyleri*
Supraclypeal protuberance with weakly and transversely rugose central area; occurs around the Gulf of California ..... *mexicanus*

** The females of *A. texanus* and *A. angelicus* cannot be separated reliably on the basis of their morphology; however, females occurring well outside the range of *A. angelicus* males are probably *A. texanus* (see map, Fig. 20).

KEY TO WEST INDIAN SPECIES

1. Males; 11 flagellomeres; scopa absent 2
Females; 10 flagellomeres; scopa on hind leg 16

2.(1) Hind femur without tooth 3
Hind femur with tooth on postero-ventral margin 4

3.(2) Lower portion of clypeus abruptly flattened, glabrous and impunctate (Figs. 109-110); metasomal terga yellow with black bands; from Hispaniola, Cuba and Jamaica ..... *kohliellus*
Lower portion of clypeus normal, not abruptly flattened, glabrous (Figs. 121-122) or impunctate; metasomal terga honey-colored; from Haiti ..... *centratus*

4.(2) Metasomal terga black or pale amber, never with metallic tints; clypeal region elongate 5
Metasomal terga with yellow and brown to black bands, often with metallic tints; clypeal region normal 9

5.(4) Head and mesosoma bright metallic green to blue 6
Head and mesosoma shiny brown-black, not metallic; from Cuba ..... *obscuratus*

6.(5) Metasomal terga dark brown to black, pale bands of tomentum conspicuous 7
Metasomal terga pale amber with brown bands, pale bands of tomentum inconspicuous or absent 8

7.(6) Sculpturing of mesosoma slightly finer than that of *viridulus,* contiguous punctures giving the mesoscutum a dark blue appearance when viewed from above; from Hispaniola ..... *hispaniolicus*
Sculpturing of mesosoma slightly coarser than that of *hispaniolicus,* subcontiguous punctures giving the mesoscutum slightly shiny green to blue reflections; from Cuba ..... *viridulus*

8.(6) Basal ridge of hind basitarsus very broadly and deeply grooved (Fig. 147); mesoscutellum extremely shiny, only weakly sculptured; from Jamaica ..... *swainsonae*
Basal ridge of basitarsus very narrow and without broad, deep groove (Fig. 149); mesoscutellum weakly shiny with contiguous punctures; from Cuba ..... *cubensis*

9.(4) Eye normal brown; pterostigma translucent amber to dark brown 10
Eye and (or) underside of pterostigma (except for dark margins) pale cream colored to opaque yellow 14

10.(9) Metasomal tergum 3 weakly to strongly metallic green to blue medially 11
Metasomal tergum 3 without metallic green to blue medially 13

11.(10) Metasomal tergum 1 with metallic green to blue tints posterolaterally 12
Metasomal tergum 1 without metallic green to blue tints posterolaterally; from Hispaniola ..... *insularis*

12.(11) Hind femur 60% as wide as long (Fig. 146); from Jamaica .. *jamaicensis*
Hind femur less than 55% as wide as long (Fig. 144); from Cuba, Hispaniola, New Providence I. and probably from Andros I. and Cat I. ..... *poeyi*

13.(10) Metasomal terga 4 and 5 with conspicuous metallic green tints medially; from San Salvador I. (=Watling I.) ..... *columbi*
Metasomal terga 4 and 5 without conspicuous metallic green tints medially (may have faint metallic tints laterally); from Puerto Rico (including Mona I. and Vieques I.) and New Providence I. ..... *viequesensis*
14.(9) Pedicel, unlike scape or flagellum, pale amber to yellow below 15
Pedicel, unlike scape or flagellum, dark brown below; from Crooked I. ..... *cyaneus*
15.(14) From Long I. ..... *sapphirinus*
From Cat I., Rum Cay, Conception I., New Providence I. and Mariguana (=Mayaguana?) I. ..... *ochromops*
16.(1) Metasomal terga black to pale amber, not metallic 17
Metasomal terga largely metallic green to blue to purple 22
17.(16) Lower portion of clypeus brown or black, metasomal terga pale amber to black, lacking yellow bands 18
Lower portion of clypeus with broad yellow band; metasomal terga with yellow bands; from Hispaniola, Cuba and Jamaica .. *kohliellus*
18.(17) Metasomal terga uniformly brown-black with narrow, white bands of tomentum 19
Metasomal terga 1 and 2 honey-colored becoming brown-black on posterior terga; from Hispaniola ..... *alayoi*
19.(18) Head and mesosoma metallic green to blue 20
Head and mesosoma shiny brown-black, not metallic; from Cuba ..... *obscuratus*
20.(19) More than 50% of interocular area above antennal sockets and below median ocellus rugose to rugulose 21
More than 50% of interocular area above antennal sockets and below median ocellus with fine, deep, contiguous punctures; from Hispaniola ..... *hispaniolicus*
21.(20) Mandible with metallic green tints basally, about as dark ferruginous-brown basally as apically; from Cuba ..... *viridulus*
Mandible without metallic green tints basally, much darker apically than basally; from Jamaica ..... *swainsonae*
22.(16) Metallic coloration dark blue or dark purple 23
Metallic coloration green 24
23.(22) Gena with fewer than 10 extremely coarse carinae; tegula and legs with some pale amber areas; from Long I. ..... *sapphirinus*
Gena with many more than 10 fine carinae; tegula and legs dark brown; from Crooked I. ..... *cyaneus*
24.(22) Eye normal brown; pterostigma translucent amber to dark brown 25
Eye or underside of pterostigma (usually both) pale cream-colored to opaque yellow; from Cat I., Rum Cay, Conception I., New Providence I. and Mariguana (=Mayaguana?) I. ..... *ochromops*
25.(24) Mandible with metallic green spot basally 26
Mandible lacking metallic green spot basally; from Puerto Rico (including Mona I. and Vieques I.) and New Providence I. .. *viequesensis*
26.(25) Metasomal sterna 3 and 4 with conspicuous medial metallic green tints 27
Metasomal sterna 3 and 4 brown, without medial metallic green tints 28

27.(26) Mesoscutum rugose laterally along parapsidal line, becoming coarsely rugose anteriorly, punctate centrally and posteriorly; from Cuba, Hispaniola, New Providence I., Cat I. and Andros I. .... *poeyi*
Mesoscutum finely punctate, with extreme antero-lateral margin rugulose; from Hispaniola ..... *insularis*

28.(26) Scopal hairs on femur and hairs on postero-ventral surface of hind tibia golden; from San Salvador I. (=Watling I.) ..... *columbi*
Scopal hairs on femur and hairs on postero-ventral surface of tibia white; from Costa Rica ..... *aenigma**

KEY TO SOUTH AMERICAN SPECIES

1. Female; 10 flagellomeres; scopa on hind leg 2
Male; 11 flagellomeres; scopa absent 10

2.(1) Mesoscutum rounded on anterior margin; lateral angle of pronotum inconspicuous and not projecting antero-laterally 3
Mesoscutum with acute upturned flange on anterior margin; lateral angle of pronotum conspicuous and projecting antero-laterally 5

3.(2) Pronotum with creamy or yellow spot at apex of posterior lobe and without carina extending postero-ventrally from lateral angle (Fig. 134) ..... *nasutus*
Pronotum without creamy or yellow spot at apex of posterior lobe and with conspicuous sharp carina extending postero-ventrally from lateral angle (Fig. 135) 4

4.(3) Metasoma black; lateral angle of pronotum rounded; 3 spatulate teeth on posterior hind tibial spur ..... *leunculus*
Metasoma amber; lateral angle of pronotum angular; 5 (rarely 4?) spatulate teeth on posterior hind tibial spur ..... *ascius*

5.(2) Metasomal terga 2 and 3 amber or black with yellow basally (best seen in posterior view) 6
Metasomal terga 2 and 3 amber or black but lacking yellow ..... *semimelleus* or *chapadensis**

6.(5) Head and mesosoma dull coppery, metallic greenish-black or bluish-black; mesoscutal pubescence dense and woolly; restricted to western South America 7
Head and mesosoma usually bright metallic green (may be coppery in Central America); mesoscutal pubescence not especially dense and finely branched; Central and South America ..... *intermedius*

7.(6) Propodeum metallic blue-black or green-black dorsally; clypeus without yellow maculations ..... *heterurus*
Propodeum metallic coppery dorsally; clypeus usually with yellow maculations 8

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* *Agapostemon aenigma* is included in this key because its similarity to West Indian species casts doubt on the correctness of its "Costa Rica" label. A specimen with identical label data belongs to the Haitian species *A. centratus*.

* The females of these species cannot be distinguished reliably (cf. *A. semimelleus*, VARIATION).

8.(7) Propodeum with coarse parallel striae dorso-laterally; clypeus without yellow maculations ..... *lanosus*
Propodeum coarsely rugose dorso-laterally; clypeus with yellow maculations 9

9.(8) Posterior half of each metasomal tergum pale amber, prepygidial fimbria brown to black ..... *mourei*
Posterior half of metasomal tergum 1 and 2 dark amber, tergum 3 brown, terga 4 and 5 and prepygidial fimbria brown-black .. *boliviensis*

10.(1) Last visible (6th) metasomal sternum with medial, button-like protrusion basally (Figs. 136-140) 14
Last visible (6th) metasomal sternum without button-like protrusion 11

11.(10) Clypeus normal, little longer than broad 12
Clypeus conspicuously concave ventrally, more than three times as broad as long (Figs. 85-87) ..... *nasutus*

12.(11) Lateral angle of pronotum prominent, acute and projecting antero-laterally; first metasomal tergum dull, with large, deep, subcontiguous punctures 13
Lateral angle of pronotum rounded; first metasomal tergum shiny, with small, shallow, scattered punctures ..... *leunculus*

13.(12) Hind femur with brown on posterior extending from base to apex (Fig. 172); gonostylus with distal stylus about twice as long as width of medial plate (Fig. 173) ..... *chapadensis*
Hind femur with brown on posterior limited to base and apex (Fig. 171); gonostylus with distal stylus little longer than width of medial plate (Fig. 174) ..... *semimelleus*

14.(10) Hind femur less than twice as long as broad; hind basitarsus extensively marked with brown or black; basal ridge and apical groove on hind basitarsus large and conspicuous (Figs. 167-170) 15
Hind femur more than twice as long as broad; hind basitarsus yellow, only rarely marked with brown; basal ridge and apical groove on hind basitarsus reduced and inconspicuous (Fig. 151) ..... *intermedius*

15.(14) Antepenultimate visible sternite (4th) without conspicuously long, contiguous, hooked setae laterally on posterior margin 16
Antepenultimate visible sternite (4th) with two or three contiguous, long (about twice length of adjacent setae), thickened, hooked setae laterally on posterior margin ..... *lanosus*

16.(15) Last visible sternite (6th) with "button" about ¼ as wide as sternite (Figs. 137, 139); basitarsus relatively broad (Figs. 167, 170) 17
Last visible sternite (6th) with "button" about ½ as wide as sternite (Fig. 140); basitarsus relatively slender (Fig. 168) ..... *inca*

17.(16) Tegula pale amber with yellow lunule anteriorly; medial plate of gonostylus large (Fig. 176) ..... *mourei*
Tegula dark ferruginous, without yellow lunule anteriorly; medial plate of gonostylus small and rounded (Fig. 177A) ..... *boliviensis*

DESCRIPTIONS, SYNONYMIES AND DISTRIBUTIONS

Agapostemon aenigma n. sp.

The name of this species refers to its mysterious affinity with certain West Indian species.

Agapostemon aenigma is known from two female specimens labeled "Costa Rica" in the same handwriting and type of label as two males of the Haitian *A. centratus*. This species appears closely related to some West Indian species and may be mis-labeled as are the similarly labeled specimens of *A. centratus*. The holotype and paratype are in the Academy of Natural Sciences, Philadelphia.

DIAGNOSIS. The female may be distinguished from other green Central American *Agapostemon* by the coarse parallel carinae on the dorsal surface of its propodeum. Among West Indian females with bright metallic green to blue metasomas, *A. aenigma* may be distinguished from females of *A. ochromops* by its lack of milky to yellowish eyes and pterostigma; from females of *A. viequesensis* by the basal metallic spot on its mandible; from females of *A. columbi* by the white (not golden) pubescence on the underside of its hind femur and tibia; and from *A. poeyi* and *A. insularis* by its lack of strong metallic tints medially on sterna 3 and 4. This species is very close to *A. insularis* and the two may eventually prove to be conspecific.

DESCRIPTION

FEMALE

General coloration of head, mesosoma and metasoma bright metallic greenish blue. **Head:** pubescence as in *A. viequesensis*. (1) *Labrum* as in *A. hispaniolicus*. (2-4) *Clypeus, interocular area* and *vertex* as in *A. viequesensis*. (5) *Gena* much more coarsely carinate than in *A. viequesensis* but not quite as coarse as in *A. poeyi*. (6) *Malar area* absent. (7-8) *Mandible* and *antenna* as in *A. poeyi*. **Mesosoma:** pubescence as in *A. viequesensis* but slightly more fuliginous on mesonotum and metanotum. (9) *Pronotum* as in *A. viequesensis* but with lateral angle and posterior lobe more angular, and with fewer and coarser (not as coarse as in *A. poeyi*) horizontal carinae postero-laterally. (10-12) *Mesoscutum, mesoscutellum* and *metanotum* as in *A. viequesensis*. (13-14) *Mesepisternum* and *metepisternum* as in *A. viequesensis* but with sculpturing very slightly coarser. (15) *Propodeum* as in *A. poeyi* but with finer sculpturing (not quite as fine as in *A. viequesensis*). (16-17) *Wing* and *tegula* as in *A. viequesensis* but with tegula darker with metallic tints more extensive. (18-20) *Fore, middle* and *hind legs* dark brown, coxae with strong metallic tints. Pubescence dark amber to brown, scopal hairs white. **Metasoma:** as in *A. viequesensis* but with faint metallic tints laterally on sterna 3 and 4 of paratype (cf. *A. insularis* ♀).

Agapostemon alayoi n. sp.

This species is named after Dr. Pastor Alayo D. of La Habana, Cuba, who has contributed significantly to our knowledge of Antillean bees.

I have seen a single specimen labeled "Acc. 1007-25/Port au Prince,/ Haiti., 1925//G. N. Wolcott/Coll." The type is in the United States National Museum, Washington, D.C.

Diagnosis. The female may be distinguished from females of *A. kohliellus* by the lack of yellow on its clypeus. No other West Indian species has females with metasomal terga 1-2 pale amber. This species is phenetically closest to *A. viridulus* and *A. hispaniolicus*. It differs from both in the coloration of its metasoma, in having a more densely punctate mesoscutellum and in being larger than females of *A. hispaniolicus*.

Description

female

General coloration of head and mesosoma metallic greenish blue, metasoma honey-colored anteriorly, brown-black posteriorly. **Head:** as in *A. viridulus* but metallic blue, with very dark fuliginous hair on interocular area and vertex. **Mesosoma:** as in *A. viridulus* but metallic blue, with slightly finer, deeper and more numerous punctures on mesoscutum and mesoscutellum. Mesoscutellum not shiny as in *A. viridulus*. Sculpturing of mesepisternum, metepisternum and propodeum slightly deeper than in *A. viridulus*. Pubescence of mesoscutum, mesoscutellum and metanotum much darker fuliginous than as in *A. viridulus*. **Metasoma:** as in *A. viridulus* but terga 1-2 pale amber instead of brown-black.

Agapostemon angelicus Cockerell

Agapostemon angelicus Cockerell 1924. Type ♀, California Academy of Sciences.

I have seen the type in San Francisco and it is from Pond Island Bay, Angel de la Guarda Island in the Gulf of California, Mexico. As the males of *A. texanus* are rare relative to those of *A. angelicus* in this region, it seems reasonable and expedient to consider this type to be conspecific with those males which differ in genitalia and color pattern from those of *A. texanus*.

Distribution. All males of *A. angelicus* have been found well within the range of the males of *A. texanus*. Owing to this sympatry and my inability to distinguish between females of *A. texanus* and *A. angelicus*, I have here considered the distribution of males and disregarded females.

Although common only in the arid regions of the southwestern United States and northern Mexico, males of *A. angelicus* have been found as far north as west-central North Dakota, as far south as northern Durango (Mexico), as far east as central Iowa, and as far west as southwestern

California. This species ranges from below sea level in Death Valley, California, to 12,000 ft. (3,658 m) on Mount Evans (timberline is at 11,700 ft.) in Colorado. The altitudinal range of *A. angelicus* is as astounding as the latitudinal range of *A. texanus.* In Arizona males of *A. angelicus* have been collected from April through November; in Kansas from June through October; and in Mexico from June through October. (Map, Fig. 20.)

Albeit uncommon, *A. angelicus* does occur in the Great Plains, where it is found together with *A. texanus* in the gallery forests of the tributaries of the Missouri and Mississippi Rivers. This habitat is the "Northern Floodplain Forest" of *Populus, Salix,* and *Ulmus* (no. 98 in Appendix A). While not as diverse as those of *A. texanus,* its habitats are numerous (39 of the 116 given by A. W. Küchler 1964—cf. Appendix A).

DIAGNOSIS. The male may be distinguished from many other species by its toothed hind femora, the apical stylus on its gonostylus, and the lack of a low medial ridge on the apical half of its last visible sternum; and from *A. texanus* by the shorter apical stylus with swollen base and enlarged apex on its gonostylus, and by the presence of a posterior stripe and absence of an anterior stripe on its hind tibia. The female may be distinguished from most other species by its bright metallic green to blue metasomal terga, its almost hyaline wings, and by the presence of two distinct sizes of mesoscutal punctures.

I have labeled females of *A. angelicus* as *"Agapostemon texanus* or *A. angelicus"* because I am unable to separate them from *A. texanus.* Sandhouse (1936) claimed that these species differ in the punctation of the mesoscutum and in the color of the pubescence. After having examined many thousands of females of these species I am forced to conclude that the variation within *A. texanus* nearly encompasses the range of variation within *A. angelicus,* thus invalidating the characters used by Sandhouse. It is probably true that the modes of *A. angelicus* characters differ from those of *A. texanus* but this cannot be demonstrated without positively identified females of both species. If one were able to positively identify *A. angelicus* females, perhaps by means of rearing, it might be possible to utilize a discriminant function to distinguish between females of the two species. Owing to the occurrence of *A. texanus* males within the range of *A. angelicus* males, I was unable to obtain females which were indisputably *A. angelicus.* Even if one were to find an area where only *A. angelicus* occurred, one could not be sure that differences between these females and females of *A. texanus* were not simply geographic variations.

VARIATION. Basing the probable identity of females on the relative abundance of males, it would seem that most females of *A. angelicus* have a slightly shinier mesoscutum and whiter pubescence than most of those of *A. texanus.* Like the males, the females of *A. angelicus* probably average

slightly smaller than those of *A. texanus,* but the variation within each species is far greater than any difference between them. In both males and females of *A. angelicus* the metallic coloration is the same green as that of the sympatric *A. texanus.* The most noticeably variable character of *A. angelicus* is the amount of melanic pigmentation on the fore coxae of males, which range in color from yellow to brown-black, but intra-locality variation is far greater than inter-locality variation.

Description

male (Figs. 73-74, 164, 181)

Males as in *A. texanus* but only about 85% as large with whiter pubescence on the mesonotum and metanotum; with dark stripe present posteriorly and absent anteriorly on its hind tibia (Fig. 164); with apical stylus on its gonostylus shorter, swollen basally, and larger apically; with medial plate on its gonostylus smaller; and with basal stylus on its gonostylus broader and blunt apically (Fig. 181).

female (Figs. 67-68)

As in *A. texanus* but always green and probably smaller with shinier mesoscutum and whiter pubescence.

Agapostemon ascius n. sp.

The name of this species comes from the Greek *skias,* or shadow. As used in Pliny, *ascius* literally means without shadow and refers to inhabitants of those regions (i.e., the tropics) where the sun is directly overhead once or twice each year.

Agapostemon ascius is known from two females labeled, "5 mi. W. Cajamarca/ Tol., COLOMBIA/ II-20-1965// Figleaf/ gourd// A. E. & M. M./ Michelbacher/ Collectors// 210.1/ 0855-/ 0905." The holotype and paratype are at the University of California, Berkeley.

Diagnosis. *A. ascius* may be distinguished from most other South American species by its lack of an acute upturned flange on the anterior margin of its mesoscutum, from *A. nasutus* by the lack of yellow on its posterior pronotal lobe, and from the closely related *A. leunculus* and *A. erebus* by its amber metasoma and 5 (rarely 4?) spatulate teeth on its posterior hind tibial spur.

Description

female

General coloration of head and mesosoma bright metallic green, metasoma amber with black at base. **Head:** (1-4) *Labrum, clypeus, interocular area* and *vertex* as in *A. nasutus.* (5) *Gena* with coarse, parallel and

anastomosing carinae. (6) *Malar area* dark amber to brown, very short. (7) *Mandible* yellowish amber basally, becoming ferruginous on apical ⅔. (8) *Antenna* black above, dark brown below, undersides of first two flagellomeres darker than others. **Mesosoma:** metallic green, never with yellow spot on posterior lobe of pronotum as in *A. nasutus*. (9) *Pronotum* with prominent carina running postero-laterally from lateral angle; lateral angle projecting slightly but not markedly as in *A. intermedius*. (10-12) *Mesoscutum, mesoscutellum* and *metanotum* as in *A. nasutus* but punctures slightly coarser and pubescence slightly more dense. (13) *Mesepisternum* very coarsely rugose anteriorly to moderately rugose posteriorly; pubescence creamy. (14) *Metepisternum* as in *A. leunculus*. (15) *Propodeum* as in *A. nasutus* but more coarsely sculptured. (16) *Wing* as in *A. nasutus*. (17) *Tegula* dark brown with transparent spot postero-laterally. (18-20) *Fore, middle* and *hind legs* as in *A. leunculus*. **Metasoma:** (21) *Terga* amber with anterior half of tergum 1, posterior half of tergum 5 and lateral margins of 2-4 dark brown to black; pubescence short, sparse and inconspicuous. (22) *Sterna* brown to brown-black with long pale hairs on exposed areas.

Agapostemon atrocaeruleus Friese

Agapostemon atrocaeruleus Friese 1916.

I am unable to locate the type of this species but have seen males and females labeled "Typus" (which only means they were identified by Friese) and they agree with his descriptions.

DISTRIBUTION. I have seen specimens from the following localities in Costa Rica: Cartago (2 ♂), San José (9 ♂, 7 ♀), San Mateo (1 ♂), Santiago de Puriscal (12 ♂, 7 ♀), and Turrialba (7 ♂, 12 ♀). Males have been collected from July through November and females from July through September. Members of this species have been collected from 1,950 ft. (594 m) in Turrialba up to 3,963 ft. (1,200 m) in San José.

DIAGNOSIS. The male may be distinguished from males of all Central American *Agapostemon* except *A. intermedius* by the very acute lateral angle and posterior lobe on its pronotum and the conspicuous flange laterally on the anterior margin of its mesoscutum; and from males of *A. intermedius* by the lack of a medial tongue-shaped process, or "button," at the base of its 6th metasomal sternum (small bump may be present, but not a distinct "button"). The female may be distinguished from females of all other species of *Agapostemon* by the combination of acutely pointed lateral pronotal angle and its almost wholly black color (usually with yellow band on clypeus and dark metallic blue tints on head and mesosoma).

Description

male (Figs. 79-80, 142, 196, 213)

General coloration of head and mesosoma bright metallic green, metasoma banded with black and yellow. **Head** (Figs. 79-80): pubescence golden to amber, becoming creamy on gena. (1) *Labrum* as in *A. texanus* but with apical portion shorter and much more acute at apex. (2) *Clypeus* with large scattered punctures on lower (yellow) half, becoming very weakly punctate and with weak horizontal carinulae on upper (green) half. (3) *Interocular area* with moderately small and deep contiguous punctures below ocelli, becoming shallower and larger (almost rugulose) at level of antennal sockets; supraclypeal protuberance with large punctures separated by about their own diameters and inclined medially. (4) *Vertex* with moderately small, deep, contiguous punctures anteriorly becoming shallower laterally, very weakly rugose between ocelli, and becoming transversely carinate posteriorly. (5) *Gena* with parallel subcontiguous weak carinae extending dorso-laterally from antero-ventral margin. (6) *Malar area* yellow, very short. (7) *Mandible* yellow with apical ⅓ ferruginous to amber. (8) *Antenna* brown to brown-black above; scape yellow below, pedicel and flagellum yellowish to amber below. **Mesosoma:** pubescence creamy, becoming golden to amber on mesonotum and metanotum. (9) *Pronotum* with small, inconspicuous, yellow spot on posterior lobe; lateral angle and posterior lobe acutely pointed, lateral angle projecting antero-laterally, sharp carina extending postero-ventrally from apex of lateral angle, and weak horizontal carinulae postero-ventrally. (10) *Mesoscutum* with large conspicuous flange laterally on anterior margin extending antero-dorsally; punctures small (slightly larger than those of *A. intermedius*), very deep and contiguous, becoming rugose antero-laterally. (11) *Mesoscutellum* with medial punctures like those of mesoscutum but separated by about their own diameters and becoming larger and much less dense laterally; large shiny area with few punctures on each side of mid-line. (12) *Metanotum* coarsely and moderately shallowly rugose. (13) *Mesepisternum* moderately coarsely rugose anteriorly, becoming finely rugose posteriorly with largest rugae extending postero-ventrally in arc from anterior margin of metepisternum. (14) *Metepisternum* with coarse, subcontiguous punctures on lower ½-⅔ becoming horizontally and irregularly rugose on upper ⅓-½. (15) *Propodeum* with propodeal carina strong and conspicuous; propodeal shield very coarsely and transversely to irregularly rugose (sometimes with scattered punctures); dorsal area very coarsely and deeply rugose; lateral area with large, deep, subcontiguous punctures and faint rugae (punctures and rugae slightly finer anteriorly than posteriorly). (16) *Wing* hyaline or slightly fuliginous, veins dark brown. (17) *Tegula* transparent amber with yellow on proximal margin and submarginally on anterior portion (some-

times small amount on posterior margin). (18) *Fore leg* yellow with dark brown basally and posteriorly on coxa; femur with brown apical spot dorsally and often with brown streak posteriorly; brown streak posteriorly on tibia. (19) *Middle leg* as fore leg but with coxa dark brown, with brown spot at apex of femur larger, and with dark brown streak on posterior of tibia extending to dorsal surface. (20) *Hind leg* (Fig. 142) with coxa bright metallic green dorsally and posteriorly, yellow ventrally; trochanter dark brown, becoming yellow ventrally; femur yellow with dark brown on proximal margin and with dark brown patch at apex; tibia with dark brown to brown-black streak antero-dorsally on apical ½-¾ and with large dark brown spot anteriorly on distal margin. **Metasoma:** (21) *Terga* 2-6 dark brown to brown-black on posterior ½-⅔ and yellow on anterior ½-⅓ (often partially concealed by overlap); tergum 1 dark brown to brown-black with yellow band antero-dorsally (often interrupted laterally); very conspicuously punctate with subcontiguous punctures largest on tergum 1, becoming progressively smaller on posterior terga. Pubescence golden to amber anteriorly on tergum 1, laterally on terga 1-7 and dorsally on terga 5-7; very short dorsally on terga 1-4, golden to fulvus on yellow bands and dark brown to brown-black on dark bands. (22) *Sterna* yellow, brown tinged with green on sternum 1 and with transverse bands on posterior margins of sterna 2-5 narrowest on sternum 2, becoming progressively wider (especially medially) posteriorly; sternum 6 with slight proximo-medial bulge but without distinct "button"; pubescence limited to scattered, moderately long, fulvus to golden hairs on exposed areas. (23) *Genitalia* (Figs. 196, 213) with ventral lobes very short and bearing brush of hairs apically.

FEMALE (Figs. 43-44)

General coloration of head and mesosoma black or blue-black, pubescence black or fuscous. **Head** (Figs. 43-44): pubescence black or nearly black, becoming fuliginous on gena. (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with transverse submarginal yellow band distally (sometimes interrupted medially or entirely absent); large scattered punctures on lower ½, becoming smaller and interspersed with short, weak, horizontal rugulae. (3) *Interocular area* with deep, contiguous, moderately small punctures below ocelli, becoming coarsely rugose above antennal sockets, becoming moderately coarsely rugose below antennal sockets; supraclypeal protuberance with deep, moderately small, scattered punctures and weak horizontal rugae. (4) *Vertex* with moderately small, deep, contiguous punctures anteriorly and laterally, becoming smaller and weaker between ocelli; transversely carinate posteriorly. (5) *Gena* with fine, contiguous, parallel carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* amber; very short, almost absent. (7) *Mandible* yellow, becoming amber to ferruginous

on basal half. (8) *Antenna* with scape and pedicel black to brown-black; flagellum brown to brown-black above, becoming amber below. **Mesosoma:** pubescence fuscous (white tomentum between posterior lobe of pronotum and mesepisternum) becoming black on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe acutely pointed, lateral angle projecting antero-laterally; with conspicuous sharp carina extending postero-ventrally from apex of lateral angle; with weak irregular horizontal rugae postero-laterally. Pubescence above lateral angle and posterior lobe black. (10) *Mesoscutum* with conspicuous flange laterally on anterior margin extending antero-dorsally; punctures small (slightly larger than those of *A. intermedius*), very deep and contiguous, becoming rugose antero-laterally. (11) *Mesoscutellum* with punctures small, deep and contiguous medially, becoming widely scattered on shiny lateral area. (12) *Metanotum* coarsely and shallowly rugose with very deep scattered punctures. (13) *Mesepisternum* moderately coarsely rugose anteriorly, becoming more finely rugose laterally and with irregular rugae extending antero-ventrally from anterior margin of metepisternum. (14) *Metepisternum* horizontally rugulose with few interconnecting rugae. (15) *Propodeum* with propodeal carina very strong and conspicuous; propodeal shield with very strong carinae extending dorso-laterally from medial groove; dorsal area with very strong, deep rugae extending postero-laterally from anterior margin (irregular medially); lateral area with numerous weak horizontal carinae anteriorly becoming fewer but larger posteriorly. (16) *Wing* as in ♂. (17) *Tegula* brown to black. (18-20) *Fore, middle* and *hind legs* brown-black to black; pubescence black dorsally, becoming dark amber below. **Metasoma:** (21) *Terga* black; punctures separated by about their diameters; pubescence very short and appressed dorsally, becoming moderately long and erect anteriorly, laterally and posteriorly; pubescence black with narrow basal band of sparse white tomentum on terga 2-4. (22) *Sterna* brown-black to black with long black hairs scattered on exposed areas.

Agapostemon boliviensis n. sp.

This species is named for the country where it is found.

The male holotype and paratype as well as the allotype are labeled, "BOLIVIA-Beni, Rur-/ renabaque, 175 mts./ 5 October 1956./ (L. Peña)." These types are in the Snow Entomological Museum at the University of Kansas.

Distribution. This species seems to be sympatric with *A. mourei*. In addition to the types, I have seen specimens in the Snow Entomological Museum with the following labels: "Cristal Mayu./ Chapare, Cochab amba Bol. 200 m./ XII-5-49 L E Pena" (2 ♂); same as preceding but collected the next day (2 ♂); "BOLIVIA-Dpto. La Paz Alta Marani, N. of

Rurrenbaque, 10 Nov/ 1956 (L. Peña)" (1 ♂). Two males in the U.S. National Museum have the following labels: "Covendo/ Bolivia/ Wm M Mann// Aug// Mulford/ BioEpl/ 1921-22" and "nr. mouth/ Rio Mapiri/ Sept// Mulford/ Bio Expl."

DIAGNOSIS. The male may be distinguished from those of most other species by the presence of a medial "button" at the base of its last visible (6th) sternum (Fig. 137). *Agapostemon boliviensis* is distinguished from the closely related *A. inca* by its lack of large hooked setae on the posterolateral margin of the antepenultimate visible (4th) sternum, from *A. mourei* and *A. inca* by the smaller and more rounded medial plate of its gonostylus, and from *A. intermedius* by its enlarged hind femur, tibia and basitarsus (Fig. 170).

The female may be distinguished from most other species by the acute lateral angle and posterior lobe of its pronotum and by the dense woolly pubescence of its mesoscutum; from those of *A. lanosus* and *A. heterurus* by the yellow maculations on its clypeus and by its more finely branched mesoscutal pubescence; from those of *A. mourei* by its slightly coarser genal striae and its darker pubescence.

DESCRIPTION

MALE (Figs. 137, 170, 177A, 215)

As in *A. mourei* but head and mesosoma bright metallic green usually with strong, dark copper tints; antenna dark brown to black with scape yellow below; tegula dark brown to brown-black; middle leg brown with narrow yellow streak anteriorly on trochanter and sometimes on tibia, and with yellow anteriorly (and usually posteriorly) on femur; hind leg (Fig. 170) with ventral ridge of basitarsus more convex; sternum 6 (Fig. 137) with proximo-medial projection, or "button," smaller and with each lateral flange approximately ½ as wide as base (as measured on transverse section through widest part of "button"); genitalia (Figs. 177A, 215).

FEMALE (Figs. 127-128)

As in *A. mourei* but with sculpturing slightly coarser and pubescence darker; metasoma brown anteriorly, becoming black posteriorly and with yellow basally on tergum 3.

VARIATION. The color of the head and mesosoma of males ranges from a bright metallic blue-green to a dark coppery luster. Furthermore, the black markings of the appendages and metasoma are often replaced by pale fawn markings. There is no obvious correlation between the color of the head and mesosoma and the color of the markings on the appendages and metasoma.

Agapostemon centratus (Vachal)

Halictus (Agapostemon) centratus Vachal 1903. Type ♂, Muséum National D'Histoire Naturelle, Paris.

A metasoma, all that remains of the holotype, is dark brown to black with broad bands of white tomentum. I have seen two males labeled "Costa Rica" and both have amber metasomas. The genitalia of the type are indistinguishable from those of the males labeled "Costa Rica." The type is from Haiti and this species resembles the West Indian *A. viridulus* group in sculpturing and genitalia. Like the similarly labeled specimens of *A. aenigma,* the two males labeled "Costa Rica" are probably from the West Indies.

Diagnosis. This species is unique in the genus inasmuch as the metasoma resembles that of females of *A. melliventris* in being amber to black with broad bands of white tomentum basally on the terga. The resemblance is so great that Sandhouse misdetermined the two males with amber metasomas as females of *A. melliventris.*

Description

male (Figs. 121-122, 152, 182, 206)

General coloration of head and mesosoma bright metallic green, metasoma amber to black with conspicuous bands of white tomentum. Pubescence of head and mesosoma white to creamy. **Head** (Figs. 121-122): (1) *Labrum* yellow with transparent margin, evenly rounded apically (not acute); basal area with conspicuous median depression. (2) *Clypeus* with shallow punctures separated by nearly twice their diameters; pubescence sparse, short. (3) *Interocular area* shallowly rugose at level of antennal sockets, becoming finely rugulose above, sparsely punctate on supraclypeal protuberance becoming shallowly rugose laterally; pubescence nearly as long as scape medially, becoming shorter laterally and appressed ventrolaterally. (4) *Vertex* with contiguous, fine punctures, becoming rugose behind ocelli; pubescence like that of interocular area. (5) *Gena* with weak, discontinuous, parallel carinulae running postero-dorsally from antero-ventral margin; pubescence dense, nearly 1.5× as long as scape postero-medially, becoming shorter anteriorly and laterally. (6) *Malar area* yellow to amber, short, with pubescence white and tomentose. (7) *Mandible* yellow, apical quarter transparent and ferruginous. (8) *Antenna.* Flagellum dark brown above, amber below and on shiny dorsal spot on apex of distal flagellomere; pedicel dark brown above, becoming light brown below; scape yellow below, dark brown above. **Mesosoma:** white pubescence moderately dense and evenly distributed (except pronotum). (9) *Pronotum* with lateral angle and posterior lobe rounded, 8-12 parallel carinulae running postero-ventrally from below lateral angle; pubescence above lateral angle

and posterior lobe like that of mesoscutum, extremely short and fine on postero-lateral area. (10) *Mesoscutum* with fine, contiguous punctures becoming finely rugulose antero-laterally. (11) *Mesoscutellum* shiny with small scattered punctures becoming larger and more numerous on lateral margins. (12) *Metanotum* with very small, sparse punctures medially and with weak, short, lateral carinulae directed postero-laterally. (13) *Mesepisternum* coarsely but shallowly rugose anteriorly, becoming finely rugose posteriorly. (14) *Metepisternum* finely, regularly and horizontally carinulate. (15) *Propodeum* rounded posteriorly; propodeal carina absent or very weak and discontinuous; weak, closely parallel carinulae running ventro-laterally from antero-dorsal margin; propodeal shield with few, weak, irregular carinulae running laterally and antero-laterally from mid-line. (16) *Wing* transparent and colorless with radius obviously darker than other veins. (17) *Tegula* transparent with metallic green on proximal margin and faint yellow transverse band. (18-20) *Fore, middle* and *hind legs* (Fig. 152) amber to fawn, slightly darker on dorsal surfaces of tibiae of middle and hind legs; all coxae metallic green. Pubescence short, creamy to amber. **Metasoma:** (21) *Terga* transparent amber with subapical brown band on tergum 1; brown band larger, darker and broader on terga 2 and 3 and covering exposed areas of terga 4-7. Broad, basal band of dense white tomentum on terga 2-5; sparse, moderately long, creamy pubescence on anterior surface of tergum 1, ventro-lateral surfaces of terga 1-6, and postero-dorsal surfaces of terga 5-7. (22) *Sterna* transparent, amber, with short creamy pubescence on exposed areas directed posteriorly. (23) *Genitalia* (Figs. 182, 206) with weak parallel carinae dorso-laterally on gonocoxa. Ventral lobes extremely large, cupped and densely fringed with short hairs.

Agapostemon chapadensis Cockerell

Agapostemon chapadensis Cockerell 1900. **Lectotype** ♂, Carnegie Museum.

? *Agapostemon castaneus* Schrottky 1902b. Type ♂? Departamento de Zoologia, São Paulo? Schrottky (1909b) synonymized the male of this species with *A. chapadensis*. Not having seen a type I cannot dispute his judgment.

? *Agapostemon azarae* Holmberg 1903. Type ♀.

? *Agapostemon argentinus* Holmberg 1903. Type ♀.

? *Agapostemon experiendus* Holmberg 1903. Type ♂.

I have seen the syntypes of *A. chapadensis* and have labeled one male lectoholotype, the other male lectoparatype and the female lectoallotype. All specimens are from Chapada. I selected a male as the lectoholotype because I am unable to distinguish the females of *A. semimelleus* and *A. chapadensis*, although the female lectoallotypes are easily distinguished.

DISTRIBUTION. This species is found in the *campos*, or tropical grasslands, of southern Brasil, of Paraguay and of northeastern Bolivia. Unlike

A. semimelleus, it has not been found in the river valleys of the eastern slopes of the Andes.

Diagnosis. The male may be distinguished from those of most other South American species by the acute lateral angle on its pronotum and lack of a "button" on its last visible sternum (6th). It may be distinguished from males of *A. semimelleus* by the longer distal stylus of its genitalia (Figs. 173-174) and by the greater amount of black on the posterior of its hind femur (Figs. 171-172).

The female cannot be distinguished from that of *A. semimelleus* (cf. *A. semimelleus,* Variation) but it may be distinguished from those of other South American *Agapostemon* by the acute upturned flange on its anterior mesoscutal margin and lack of basal yellow bands on its metasomal terga.

Description

male (Figs. 172-173, 219)

General color of head and mesosoma bright metallic green, metasoma banded with black and yellow. Like male of *A. semimelleus* but for the following features. **Mesosoma:** (18) *Fore leg* yellow with brown (sometimes with slight metallic tints) posteriorly on trochanter, femur and tibia. (19) *Middle leg* yellow with brown on coxa, basitarsus, posterior of trochanter and tibia, and posterior of apical ½ of femur. (20) *Hind leg* (Fig. 172) yellow with upper ½ of coxa metallic, with brown on trochanter, on posterior and apex of femur, on posterior and antero-dorsal regions of tibia, and on all but antero-ventral region of basitarsus. **Metasoma:** (22) *Sterna* 2-5 brown with amber posterior margins and sometimes with yellow on anterior margins, sternum 1 amber with metallic tints basally, and sternum 6 amber becoming brown on anterior margin. (23) *Genitalia* (Figs. 173, 219) ventral lobes very short with apical brush of long stiff hairs. Distal stylus about twice as long as width of medial plate.

female

Like that of *A. semimelleus* (cf. *A. semimelleus,* Variation).

Agapostemon cockerelli Crawford

Agapostemon cockerelli Crawford 1901. Type ♀, U.S. National Museum.
Agapostemon martini Cockerell 1927. Males only (misidentified).

I have examined the types of *Agapostemon cockerelli* Crawford and *Agapostemon femoratus* Crawford (1901) in Washington, D.C. and, contrary to the opinions of Sandhouse (1936) and Michener (1951), find them specifically distinct. The males (paratypes) of *Agapostemon martini* Cockerell (1927) were misdetermined and belong in *A. cockerelli. Nomia cillaba* Cameron (1902), listed by Michener (*In* Muesebeck, et al., 1951) as a

possible synonym of *Agapostemon cockerelli,* does not belong in the genus *Agapostemon* (cf. *Excluded Species*).

DISTRIBUTION (Fig. 2). *Agapostemon cockerelli* occurs as far north as Pat Creek, Park Co., Wyoming; as far south as Petlalcingo, Puebla, Mexico; as far east as Tehuacan, Mexico; and as far west as Wickenburg, Maricopa Co., Arizona. Most abundant at elevations of 4,500-7,500 ft. (1,372-2,286 m), this species has been collected as high as 8,000 ft. (2,438 m) on Pine Top Mountain, Culberson Co., Texas, and as low as 2,100 ft. (640 m) in Big Bend National Park, Brewster Co., Texas. In Mexico it is apparently restricted to the central plateau, where it has been collected as high as 7,300 ft. (2,225 m) 20 miles north of Zacatecas, Zacatecas, and as low as 1,850 ft. (564 m) in Boquillas del Carmen, Coahuila. In the United States females of *A. cockerelli* have been collected from March through October and males from April through November. In Mexico females have been collected from June through October and males from April through December.

DIAGNOSIS. The male may be distinguished from males of many species by its toothed and conspicuously inflated hind femora, the lack of an apical stylus on its gonostylus, or by its nearly hyaline wings; from males of *A. radiatus* by the basal ridge on its basitarsus; and from males of *A. femoratus* by the much smaller basal ridge on its hind basitarsus (Figs. 162-163). The female may be distinguished from females of many species by its metallic green metasomal terga, its coarsely punctate or rugose mesoscutum without punctures of two distinct sizes, and its nearly hyaline wings; and from females of *A. femoratus* by its largely punctate (rugose only anteriorly and laterally) mesoscutum. The female cannot be morphologically differentiated from females of *A. radiatus* but may be distinguished by its southwestern distribution.

DESCRIPTION

MALE (Figs. 107-108, 162)

General color of head and mesosoma bright green to blue-green, metasoma with black and yellow bands. **Head** (Figs. 107-108): pubescence white, becoming pale yellowish on vertex and sometimes on interocular area; more dense than in *A. radiatus.* (1) *Labrum* as in *A. texanus.* (2-5) *Clypeus, interocular area, vertex* and *gena* as in *A. radiatus* but with slightly coarser and shallower sculpturing. (6-7) *Malar area* and *mandible* as in *A. radiatus.* (8) *Antenna* as in *A. radiatus* but with underside of flagellum pale amber to yellowish and with upper side of apical half of apical flagellomere pale amber to yellow. **Mesosoma:** pubescence white, commonly becoming yellowish on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe slightly more angular than in *A. radiatus* and with sculpturing weaker than in *A. radiatus.* (10-15) *Mesoscutum,*

mesoscutellum, metanotum, mesepisternum, metepisternum and *propodeum* as in *A. radiatus* but with sculpturing shallower and slightly finer. (16-17) *Wing* and *tegula* as in *A. radiatus* but slightly paler. (18-19) *Fore* and *middle legs* as in *A. radiatus* but with brown maculations reduced (may be absent on fore leg). (20) *Hind leg* (Fig. 162) as in *A. radiatus* but with trochanter yellow with femur and tibia more swollen and with small basal ridge and apical groove on basitarsus. **Metasoma:** (21-22) *Terga* and *sterna* as in *A. radiatus* but with dark brown or black areas reduced, and with stronger metallic tints postero-laterally on terga 3-4. (23) *Genitalia* indistinguishable from those of *A. femoratus*.

FEMALE (Figs. 59-60)

General coloration of head, mesosoma and metasoma bright metallic green to blue-green. **Head** (Figs. 59-60): pubescence white, commonly with faint yellow tints on vertex. (1) *Labrum* as in *A. texanus*. (2-4) *Clypeus, interocular area* and *vertex* as in *A. radiatus* but with sculpturing slightly shallower and slightly finer. (5) *Gena* as in *A. radiatus* but with genal carinae usually slightly coarser. (6-7) *Malar area* and *mandible* as in *A. radiatus*. (8) *Antenna* as in *A. radiatus* but often paler on underside of flagellum and with yellowish amber at base and apex of scape. **Mesosoma:** pubescence white, becoming slightly yellowish to fuliginous on mesonotum and metanotum. (9) *Pronotum* as in *A. radiatus* but with sculpturing slightly weaker. (10-13) *Mesoscutum, mesoscutellum, metanotum, mesepisternum* as in *A. radiatus* but with sculpturing slightly coarser. (14) *Metepisternum* as in *A. radiatus* but irregularly anastomosing carinae with greater tendency to rugose condition. (15) *Propodeum* as in *A. radiatus* but with slightly finer rugae on propodeal shield; dorsal surface with much shallower sculpturing and more commonly rugose or with more frequently anastomosing carinae. (16) *Wing* as in *A. radiatus* but slightly paler. (17) *Tegula* as in *A. radiatus* ♂ but slightly paler. (18-20) *Fore, middle* and *hind legs* as in *A. radiatus* but with pubescence paler; with yellow markings on fore leg and middle leg; and usually with more extensive yellow markings anteriorly on fore tibia. **Metasoma:** (21) *Terga* as in *A. radiatus* but bands of white tomentum on terga 2-4 slightly broader and more dense. (22) *Sterna* as in *A. radiatus* but rarely with weak metallic tints on sternum 4.

Agapostemon coloradinus (Vachal)

Agapostemon coloradensis Crawford 1901. **Lectotype*** ♀, U.S. National Museum.
Halictus (Agapostemon) coloradinus Vachal 1903.

When Vachal placed *Agapostemon* in the genus *Halictus, Agapostemon*

* The specimen is labeled "Lectotype." Although I have not been able to find a lectotype designation in the literature, I accept this specimen as a lectotype and formalize it by so designating it here.

coloradensis Crawford became a junior secondary homonym of *Augochlora coloradensis* Titus. Vachal renamed the former, *Halictus (Agapostemon) coloradinus.* Few workers agreed with Vachal's placement of *Agapostemon* as a subgenus of *Halictus,* but the International Code of Zoological Nomenclature (anonymous, 1964) states (Article 59c) that secondary homonyms rejected before 1961 cannot be revived, contrary opinions (Cockerell, 1937a and Michener, *In* Muesebeck, et al., 1951) notwithstanding.

Sandhouse (1936) included *Agapostemon tyleri* Cockerell and *Agapostemon martini* Cockerell in *Agapostemon coloradinus* (Vachal), but having examined the types I find her decisions unjustified (cf. *A. tyleri*).

DISTRIBUTION (Fig. 3). This is by far the rarest of the North American species and its range is more restricted than that of any other North American species. I have seen fewer than 300 specimens, from the high, western plains of South Dakota, Nebraska, Kansas, Oklahoma and Texas and from both the plains and mountains of New Mexico, Colorado, Wyoming and central Utah. Females have been collected from May through October and males from August through October. Specimens have been collected as low as 2,060 ft. (628 m) in Rush Co., Kansas and as high as 10,600 ft. (3,231 m) at Echo Lake, Mt. Evans, Colorado.

DIAGNOSIS. The male may be distinguished from all other North American species except *A. tyleri* by the lack of yellow maculations on its dark brown to black metasomal sterna; from *A. tyleri* by its larger size, by the brown streak on the central ⅔ of the length of the posterior surface of its hind tibia (Figs. 159-160), and by its more slender penis valve which has a conspicuous row of hairs on its dorsal crest (Figs. 226-227). The female may be distinguished from many other species occurring north of Mexico by its black metasoma and the lack of yellow on its clypeus; from *A. virescens* by its finer and more numerous genal carinulae (2-3 per 0.25 mm in *A. virescens* and 5-6 per 0.25 mm in *A. coloradinus*); and from *A. tyleri* by its brown wings, paler tegulae and less shiny supraclypeal protuberance. This species is very close phenetically to *A. tyleri.*

DESCRIPTION

MALE (Figs. 99-100, 160, 185, 199, 226)

General coloration of head and mesosoma bright metallic blue to greenish blue, metasoma with black and pale yellow to creamy bands. **Head** (Figs. 99-100): pubescence snowy white. (1) *Labrum* as in *A. texanus* but more rounded at apex. (2) *Clypeus* as in *A. virescens* but punctures shallower and pubescence more dense. (3) *Interocular area* with coarse contiguous punctures (some specimens finely rugose around antennal sockets); supraclypeal protuberance as in *A. virescens.* (4) *Vertex* as in *A. virescens.* (5) *Gena* as in *A. virescens* but with carinae much finer. (6) *Malar area* yellow,

never amber; short. (7) *Mandible* as in *A. virescens*. (8) *Antenna* dark brown to brown-black above with apex of apical flagellomere amber; flagellum amber below and underside of scape and pedicel yellow (scape of some specimens from Boulder, Colorado, area black with yellow apically on underside). **Mesosoma:** pubescence snowy white. (9) *Pronotum* as in *A. virescens* but with weaker sculpturing. (10) *Mesoscutum* as in *A. virescens* but with finer punctures and with anterior margin punctate. (11-13) *Mesoscutellum, metanotum* and *mesepisternum* as in *A. virescens* but with finer sculpturing. (14) *Metepisternum* rugose or with irregularly anastomosing carinae. (15) *Propodeum* with propodeal carina weak, often broadly interrupted laterally; propodeal shield finely and weakly rugulose; finely rugose dorsally and postero-laterally becoming punctate antero-laterally. (16) *Wing* as in *A. virescens* but paler and with darker radial vein. (17) *Tegula* as in *A. virescens* but slightly paler and transparent. (18-19) *Fore* and *middle legs* as in *A. virescens* but with brown-black markings of tibiae and femora more extensive and sometimes with yellow apically on ventral surface of trochanter. (20) *Hind leg* (Fig. 160) as in *A. virescens* but tibia with brown streak on apical ½ of posterior surface, femur with brown streak entire length of posterior surface, trochanter usually with yellow spot apically on antero-ventral surface, and tooth on femur directed distally. **Metasoma:** (21) *Terga* brown-black with creamy bands on basal halves of terga 2-5 and centrally on tergum 1 (commonly interrupted medially on tergum 1); pubescence short dorsally on terga 1-4, black on dark bands and white on creamy bands; moderately long and white elsewhere. (22) *Sterna* brown to brown-black, usually with faint carina medially on apical ½ of sternum 6; moderately long white hairs scattered on exposed areas. (23) *Genitalia* (Figs. 185, 199, 226) as in *A. virescens* but with smaller fold on medial plate of gonostylus and with conspicuous hairs on prominent dorsal crest of penis valve.

female (Figs. 49-50)

General coloration of head and mesosoma bright metallic blue to blue-green, metasoma black with white hair bands. **Head** (Figs. 49-50): (1) *Labrum* as in *A. texanus* but with distal keel slightly broader. (2-4) *Clypeus, interocular area* and *vertex* as in *A. virescens* but with sculpturing slightly finer. (5) *Gena* as in *A. virescens* but with much finer and more numerous (5-6 per 0.25 mm) carinulae. (6) *Malar area* dark ferruginous to brown-black; very short, almost absent. (7) *Mandible* very dark amber with apical ⅓ darker ferruginous and base almost black (with very faint metallic tints on some specimens). (8) *Antenna* brown-black, lower half of flagellum usually slightly paler brown than upper ½. **Mesosoma:** snowy white pubescence sometimes very slightly fuliginous on mesonotum and meta-

notum. (9-15) *Pronotum, mesoscutum, mesoscutellum, metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. virescens* but with sculpturing slightly shallower and finer. (16) *Wing* brown in contrast to that of male; unlike that of *A. splendens,* not markedly darker on distal borders; radius brown-black, other veins and pterostigma dark brown. (17) *Tegula* as in *A. virescens.* (18-20) *Fore, middle* and *hind legs* as in *A. virescens* but with pubescence basally on antero-dorsal surface of hind leg slightly paler (usually amber but may be dark brown). **Metasoma:** (21-22) *Terga* and *sterna* as in *A. virescens.*

Agapostemon columbi n. sp.

This species is named after Christopher Columbus who first landed in the New World on San Salvador Island (=Watling I.).

I have seen one male and one female of *A. columbi.* The male is labeled, "Watlings [*sic*] Is./Bahama Islands/W. W. Worthington/III.13.1909//Carn. Mus./Acc. 3960." The female is labeled, "Watling Is./Bahama Islands/W. W. Worthington/III.20.1909//Carn. Mus./Acc. 3960." The male holotype and the allotype are both at the Carnegie Museum, Pittsburgh, Pennsylvania.

DIAGNOSIS. The female may be distinguished from *A. viridulus, A. obscuratus, A. hispaniolicus, A. swainsonae, A. alayoi* and *A. kohliellus* by its metallic metasomal terga; from *A. sapphirinus, A. cyaneus* and *A. ochromops* by its lack of milky yellowish eyes and pterostigma; from *A. viequesensis* by the metallic green tints on the base of its mandible; from *A. poeyi* and *A. insularis* by its lack of metallic green tints on metasomal sterna 3 and 4; and from *A. aenigma* by the golden (rather than white) pubescence on the undersides of its hind femur and tibia.

The male may be distinguished from *A. viridulus, A. obscuratus, A. hispaniolicus, A. swainsonae* and *A. cubensis* by its lack of an elongate clypeal area; from *A. kohliellus* and *A. centratus* by the tooth on its hind femur; from *A. sapphirinus, A. cyaneus* and *A. ochromops* by its lack of milky to yellowish eyes and pterostigma; from *A. insularis, A. jamaicensis* and *A. poeyi* by its lack of metallic green or blue medially on metasomal tergum 3; and from *A. viequesensis* by its conspicuous metallic green tints medially on metasomal terga 4-5. Both males and females of *A. columbi* are slightly larger than those of other members of the *A. viequesensis* species group.

DESCRIPTION

MALE

General coloration of head and mesosoma bright metallic blue-green, metasoma dark brown with narrow yellow bands. **Head:** as in *A. viequesensis* but with pubescence amber on interocular area and vertex.

Mesosoma: pubescence on mesonotum and metanotum pale amber, elsewhere pale yellowish to creamy. (9) *Pronotum* as in *A. viequesensis* but with fewer and coarser horizontal carinae on postero-lateral area, and with lateral angle and posterior lobe slightly more angular. (10-14) *Mesoscutum, mesoscutellum, metanotum, mesepisternum* and *metepisternum* as in *A. viequesensis* but with coarser sculpturing as in *A. poeyi* (but not as coarse). (15) *Propodeum* with sculpturing much coarser than in *A. viequesensis* and with prominent carinae extending postero-laterally from posterior margin of metanotum. (16) *Wing* as in *A. viequesensis* but slightly darker and with darker veins and pterostigma. (17) *Tegula* as in *A. viequesensis* but with transparent amber portion slightly darker. (18-20) *Fore, middle* and *hind legs* as in *A. viequesensis.* **Metasoma:** pubescence as in *A. viequesensis.* (21) *Terga.* Tergum 1 dark amber on anterior ½, dark brown on posterior dorsal area, and with yellow band centrally, broadly interrupted medially. Terga 2-3 dark brown with yellow band on anterior ⅓. Terga 4-7 like 2-3 but with conspicuous metallic tints on dark brown areas. (22) *Sterna* as in *A. viequesensis.* (23) *Genitalia* as in *A. viequesensis* but with apex of distal stylus on gonostylus slightly enlarged, but not so much as in *A. poeyi.*

FEMALE

General coloration of head, mesosoma and metasoma bright metallic blue-green to blue (metasoma with purple-brown tints). **Head:** pubescence white, only very faintly fuliginous on vertex. (1) *Labrum* as in *A. hispaniolicus* (cf. *A. viequesensis*). (2-5) *Clypeus, interocular area, vertex* and *gena* as in *A. viequesensis* but with sculpturing much coarser, although not as coarse as in *A. poeyi.* (6-8) *Malar area, mandible* and *antenna* as in *A. viequesensis* but with metallic spot at base of mandible. **Mesosoma:** as in *A. viequesensis* but pubescence paler on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe slightly more angular than in *A. viequesensis,* although not so much as in *A. poeyi;* and with postero-lateral horizontal carinae fewer in number and coarser than in *A. viequesensis* although not as few and as coarse as in *A. poeyi.* (10) *Mesoscutum* with punctures slightly coarser than in *A. viequesensis,* but not nearly as coarsely sculptured as in *A. poeyi.* (11) *Mesoscutellum* as in *A. viequesensis* but less shiny and with punctures deeper and denser. (12-15) *Metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. poeyi* but with finer sculpturing, although not as fine as in *A. viequesensis.* (16) *Wing* as in ♂. (17) *Tegula* as in *A. viequesensis.* (18-20) *Fore, middle* and *hind legs* as in *A. viequesensis* but with pubescence amber, becoming brown-black antero-dorsally on tibia and basitarsus (not as dark on latter) of hind leg. **Metasoma:** as in *A. viequesensis* but with metallic areas bluer and nonmetallic areas darker.

Agapostemon cubensis n. sp.

This species is named for the island of Cuba where it is found.

I have seen a single male labeled, "Cuba 5.K./S. of Pinar Rio,/ Sept. 12-23 '13." The type is in the American Museum of Natural History, New York.

DIAGNOSIS. The male of this species may be distinguished from *A. kohliellus* and *A. centratus* by its toothed hind femora; from *A. viridulus, A. obscuratus* and *A. hispaniolicus* by its pale amber and brown banded basal metasomal terga; from *A. swainsonae* by its small and narrowly grooved basitarsal ridge; and from males of *A. poeyi, A. viequesensis, A. cyaneus, A. sapphirinus, A. ochromops, A. columbi, A. insularis* and *A. jamaicensis* by its elongate clypeal area.

DESCRIPTION

MALE (Figs. 119-120, 149)

General coloration of head and mesosoma shiny, metallic blue and green, metasoma pale amber and brown. **Head** (Figs. 119-120): pubescence white. (1) *Labrum* as in *A. viridulus* but white and darkened only centrally. (2) *Clypeus* metallic blue above, white below; elongate as in *A. viridulus;* shiny and sparingly punctate medially, becoming more densely punctate laterally; pubescence sparse. (3) *Interocular area* metallic blue; shallow contiguous punctures below median ocellus, shallowly and finely rugose just above and at level of antennal sockets, becoming shiny with scattered punctures below antennal sockets, supraclypeal protuberance shiny and sparsely punctate and with weak transverse carinulae; pubescence between antennal sockets about ⅔ as long as scape, becoming shorter laterally, dorsally and ventrally; tomentose ventro-laterally, near malar area. (4) *Vertex* metallic blue, changing to blue-green posteriorly; punctures very fine (finer than in *A. viridulus*), shallow anteriorly and laterally, becoming rugose posteriorly; area between ocelli sparsely and shallowly punctate; pubescence white, not fuliginous as in *A. viridulus.* (5) *Gena* metallic blue-green in contrast to metallic blue of clypeus, interocular area and vertex; rugae as in *A. viridulus* but weaker; pubescence as long as scape posteromedially, becoming shorter laterally, anteriorly and dorsally. (6-8) *Malar area, mandible* and *antenna* as in *A. viridulus* but with white replacing yellow. **Mesosoma:** pubescence as in *A. viridulus* but white on mesonotum and metanotum. (9) *Pronotum* as in *A. viridulus* but blue dorsomedially, becoming blue-green ventro-laterally. (10) *Mesoscutum* metallic blue with very fine punctures, slightly shallower and less dense than in *A. viridulus* and becoming weakly rugulose anteriorly. (11) *Mesoscutellum* metallic blue-green, punctures as in *A. viridulus* but slightly shallower. (12) *Metanotum* metallic blue-green, with sculpturing as in *A. viridulus.*

(13) *Mesepisternum* metallic blue-green antero-dorsally becoming green posteriorly and ventrally, with sculpturing as in *A. viridulus* but slightly coarser. (14) *Metepisternum* metallic blue-green dorsally, becoming green ventrally, with sculpturing as in *A. viridulus* but slightly coarser. (15) *Propodeum* metallic green, with sculpturing as in *A. viridulus.* (16) *Wing* as in *A. viridulus* but with veins not as dark. (17) *Tegula* as in *A. viridulus* but transparent portion amber and metallic tints blue. (18-19) *Fore* and *middle legs* as in *A. viridulus* but with pale amber replacing dark brown. (20) *Hind leg* (Fig. 149) with coxa and trochanter as in *A. viridulus;* femur amber with white antero-ventrally, on basal ⅔ antero-dorsally, and on postero-ventral margin between tooth and distal margin; tibia pale amber ventrally becoming pale brown dorsally; tarsus amber. Femur less swollen than in *A. viridulus,* basitarsus with narrow basal ridge much smaller than in *A. viridulus,* apical groove much narrower and shallower than in *A. viridulus.* Pubescence as in *A. viridulus.* **Metasoma:** (21) *Terga.* Tergum 1 pale amber with narrow band of pale brown anteriorly on dorsal surface; tergum 2 pale amber with central brown band darker and broader than on preceding tergum 1; tergum 3 with broad dark brown band centrally, pale amber basally, and brown apically; terga 4-7 brown-black basally, becoming brown apically. Moderate to long white hairs scattered on ventro-lateral margins, anteriorly on tergum 1, and posteriorly on terga 5-7; short, dense, simple, prostrate hairs on terga 1-5 brown and inconspicuous; thin, white inconspicuous tomentum basally on terga 1-6 (usually hidden by preceding terga). (22) *Sterna* as in *A. viridulus* but amber with subapical, pale brown band narrow on sternum 3, becoming broader and darker on sterna 4-6. (23) *Genitalia* (examined dry) as in *A. viridulus* but with about ½ as many grooves on gonocoxa.

Agapostemon cyaneus n. sp.

The name of this species refers to the dark blue color of the female.

I have seen ten specimens (7 ♂, 3 ♀) of *A. cyaneus.* The female holotype, the allotype and seven paratypes are labeled, "Bahamas/Crooked Isl./1-2 Mar//Utowana/Exp. 1934," and one male paratype is labeled, "Bahamas/Crooked Isl./20-II//Greenway/coll." All of the types are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Diagnosis. Both males and females may be distinguished from all other West Indian species, except *A. sapphirinus* and *A. ochromops,* by their milky to yellowish eyes and pterostigma. The male of *A. cyaneus* may be distinguished from *A. sapphirinus* and *A. ochromops* by its pedicel which is yellow to amber below (not dark brown). The female of *A. cyaneus* may be distinguished from *A. ochromops* by its very dark blue color, and from *A. sapphirinus* by its finely carinate gena.

DESCRIPTION

MALE

General coloration of head and mesosoma dark metallic green to blue, metasoma black with pale yellow bands. **Head:** darker than in *A. viequesensis* and with paler eyes; pubescence as in *A. viequesensis*. (1-7) *Labrum, clypeus, interocular area, vertex, gena, malar area* and *mandible* as in *A. viequesensis*. (8) *Antenna* as in *A. viequesensis* but with black on upper surface replaced by yellow on distal ½ of apical flagellomere and basal ⅓-¼ of scape, with underside of flagellum pale amber to yellow, and with underside of scape dark brown to black. **Mesosoma:** pubescence as in *A. viequesensis*. (9-15) *Pronotum, mesoscutum, mesoscutellum, metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. viequesensis* but with very slightly coarser sculpturing. (16) *Wing* as in *A. viequesensis* but with pale yellow pigment on pterostigma and underside of larger veins. (17) *Tegula* as in *A. viequesensis* but with amber replaced by dark brown. (18-20) *Fore, middle* and *hind legs* as in *A. viequesensis* but with brown-black replacing amber, with yellow areas paler, with brown-black posterodorsally on apex and base of middle femur (and sometimes fore femur), and with average size of basal ridge of basitarsus slightly greater. **Metasoma:** pubescence as in *A. viequesensis*. (21) *Terga* brown-black with narrow, pale yellow bands basally on terga 2-7 (those on posterior terga usually hidden by overlap), and centrally on tergum 1 (often interrupted medially); apex of pygidium nearly as acute as in *A. ochromops* (Fig. 225). (22) *Sterna* as in *A. viequesensis* but brown-black to amber, and sometimes with metallic spot medially on transverse submarginal ridge of sternum 4. (23) *Genitalia* as in *A. poeyi* but distal stylus on gonostylus not as swollen at apex (cf. *A. viequesensis*).

FEMALE

General coloration of head, mesosoma and metasoma very dark metallic bluish purple. **Head:** as in *A. viequesensis* but with eyes whitish, pubescence wholly white, mandibles brown-black with metallic tints at base and ferruginous apically. **Mesosoma:** as in *A. viequesensis* but with pubescence of mesonotum and metanotum white and fuliginous dorsally on middle tibia, hind tibia and apex of hind femur; with wings as in ♂; and with tegula brown-black with metallic tints antero-basally. **Metasoma:** as in *A. viequesensis* but with basal bands of white tomentum on terga broader and denser, and with sterna very dark brown with faint metallic tints.

Agapostemon erebus n. sp.

This species is named after the Greek god Erebus, personification of darkness and brother of Night.

The female holotype is in the California Academy of Sciences, San Francisco. It is labeled, "El Salvador/Mt. San Salvador/VII-8-1963//M. E. Irwin &/D. Q. Cavagnaro/Collectors." A second female is in the University of Kansas collection labeled, "Guatemala 6.3 mi./NE. Escuintla/30 July 1966/U. Kansas Mex. Exped."

Diagnosis. *A. erebus* may be distinguished from the similarly colored females of *A. atrocaeruleus* by its rounded lateral pronotal angle and its coarse genal carinae. It may be distinguished from those females of *A. nasutus* with dark blue head and thorax by the prominent carina running postero-ventrally from the lateral angle of its pronotum, by the lack of yellow on the posterior lobe of its pronotum, and by its coarse genal carinae. It seems most closely related to *A. leunculus* but differs from females of this species by its blue-black head and thorax and shiny lateral area on its mesoscutellum.

Description

female

General coloration of head and mesosoma very dark blue to black and only slightly metallic, metasoma black with narrow bands of white pubescence dorsally. **Head:** (1-4) *Labrum, clypeus, interocular area* and *vertex* as in *A. nasutus* but with pubescence predominantly black. (5) *Gena* with coarse, parallel and anastomosing carinae and whitish pubescence as in *A. leunculus*. (6) *Malar area* black, short. (7) *Mandible* yellow basally, becoming ferruginous on apical ⅔. (8) *Antenna* as in *A. leunculus*. **Mesosoma:** (9) *Pronotum* as in *A. nasutus* but dark blue and with prominent carina running postero-ventrally from lateral angle. (10) *Mesoscutum* dark purple-blue marginally, dull green-black centrally; sculpturing as in *A. nasutus* but slightly finer; pubescence black. (11) *Mesoscutellum* dark purple-black; punctation as in *A. nasutus* but with lateral shiny area more shiny and conspicuous; pubescence black. (12) *Metanotum* dark purple-black, rugulose; pubescence black. (13) *Mesepisternum* purple-black; sculpturing as in *A. leunculus;* pubescence dark fuliginous on dorsal ⅓, becoming white below. (14-15) *Metepisternum* and *propodeum* dark blue, sculpturing as in *A. nasutus* but slightly coarser; pubescence white, sparse except around and posterior to propodeal spiracle. (16) *Wing* transparent, not darkened apically, radius scarcely darker than other veins. (17) *Tegula* black, dark transparent brown postero-laterally. (18) *Fore leg* brown-black with small yellow spot at base of tibia; pubescence of coxa and trochanter white, remainder dark brown to black. (19-20) *Middle* and *hind legs* brown-black; pubescence similar in color to that of fore leg, but scopal hairs creamy. **Metasoma:** (21-22) *Terga* and *sterna* as in *A. leunculus* (on the holotype the normally hidden, pale brown basal areas of terga are exposed).

Agapostemon femoratus Crawford

Agapostemon femoratus Crawford 1901, Type ♂, U.S. National Museum.
Agapostemon californicus Crawford 1901. Females only (misidentified).

Sandhouse (1936) and Michener (1951) both considered *A. femoratus* synonymous with *A. cockerelli* Crawford (1901), but after examining the types of both species in Washington, D.C., I concluded that they are specifically distinct. The females (paratypes) of *Agapostemon californicus* Crawford (1901) were misdetermined and belong in *A. femoratus.*

DISTRIBUTION. *Agapostemon femoratus* occurs as far north as Chilcotin, British Columbia, Canada; as far south as San Vicente, Baja California, Mexico; as far west as the coast of California; and as far east as Williston, North Dakota. In the northern part of the range (Washington), females have been collected from April through October and males from June through October. In California south of Los Angeles, females have been collected from February through November, and males in March and May through November. This species is equally abundant at high and low elevations. *A. femoratus* has been collected as high as 10,150 ft. (3,094 m) at Blanco's Corral, Mono Co., California; 10,000 ft. (3,048 m) at Blue Ridge Fire Lookout, Fremont Co., Wyoming; 9,200 ft. (2,804 m) at Warner Ranger Station, Grand Co., Utah; and 8,600 ft. (2,541 m) on Hart Mountain, Lake Co., Oregon. (See map, Fig. 4.)

DIAGNOSIS. The male may be distinguished from many other species by its conspicuously inflated and toothed hind femora, the large and conspicuous apical groove on its hind basitarsus, or its nearly hyaline wings; from *A. radiatus* by the large basal ridge on its basitarsus; and from *A. cockerelli* by its much larger basal ridge on its hind basitarsus and much more inflated hind leg (Figs. 162-163). The female may be distinguished from other species by its metallic green metasomal terga or its coarsely rugose mesoscutum.

DESCRIPTION

MALE (Figs. 101-104, 163, 194, 202)

General color of head and mesosoma bright metallic green, metasoma with black and yellow bands. **Head** (Figs. 101-104): pubescence white, usually yellowish on vertex and often pale yellow on interocular area, denser than in *A. radiatus.* (1) *Labrum* as in *A. texanus.* (2-7) *Clypeus, interocular area, vertex, gena, malar area* and *mandible* as in *A. radiatus.* (8) *Antenna* as in *A. radiatus* but with underside of flagellum pale amber to yellowish and with upper side of distal ½ of apical flagellomere pale amber to yellow. **Mesosoma:** pubescence white, commonly becoming yellowish on mesonotum and metanotum. (9) *Pronotum* as in *A. radiatus* but with lateral angle and posterior lobe slightly more angular, and sculp-

turing weaker. (10-15) *Mesoscutum, mesoscutellum, metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. radiatus,* but with sculpturing slightly shallower. (16-17) *Wing* and *tegula* as in *A. radiatus* but paler. (18) *Fore leg* as in *A. radiatus* but lacking brown stripe on tibia. (19) *Middle leg* as in *A. radiatus* but with brown tibial stripe very reduced. (20) *Hind leg* (Fig. 163) as in *A. radiatus* but with trochanter yellow; brown stripe on tibia reduced; femur, tibia and basitarsus swollen (femur subglobose); and basitarsus with very large, slightly sinuate basal ridge and large broad apical groove. **Metasoma:** (21-22) *Terga* and *sterna* as in *A. radiatus* but with dark brown or black areas reduced, and with stronger metallic tints postero-laterally on terga 3-4. (23) *Genitalia* (Figs. 194, 202) with gonocoxite partially fused with gonobase; gonostylus with large medial plate but lacking apical and basal styli; ventral lobe of gonocoxite moderately large and with distal fringe of hairs.

FEMALE (Figs. 57-58)

General coloration of head, mesosoma and metasoma bright metallic blue-green to blue. **Head** (Figs. 57-58): pubescence white, commonly very pale yellow on vertex. (1) *Labrum* as in *A. texanus.* (2-4) *Clypeus, interocular area* and *vertex* as in *A. radiatus* but with sculpturing slightly deeper and more coarse. (5) *Gena* as in *A. radiatus.* (6) *Malar area* dark brown to brown-black; short. (7) *Mandible* as in *A. radiatus* but with pigment creamy and less opaque. (8) *Antenna* as in *A. radiatus* but with flagellum slightly paler on underside. **Mesosoma:** pubescence white, becoming very faintly yellowish on some specimens. (9) *Pronotum* as in *A. radiatus* but with slightly finer sculpturing. (10) *Mesoscutum* very coarsely and deeply rugose, becoming coarsely and contiguously punctate postero-medially. (11-15) *Mesoscutellum, metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. radiatus* but with sculpturing slightly coarser; dorsal area of propodeum with carinae more commonly anastomosing or rugose. (16) *Wing* as in *A. radiatus.* (17) *Tegula* as in *A. radiatus* ♂ but much paler. (18-20) *Fore, middle* and *hind legs* as in *A. radiatus.* **Metasoma:** (21) *Terga* as in *A. radiatus.* (22) *Sterna* as in *A. radiatus* but darker and never with metallic tints on sternum 4.

Agapostemon heterurus Cockerell

Agapostemon heterurus Cockerell 1917 (a). Type ♀, U.S. National Museum.

In addition to the type and paratype, I have seen a third specimen of *A. heterurus.* All three of these specimens are females; all are in the U.S. National Museum; all are labeled, "Palcazul Peru//Collection/Rosenberg."

Diagnosis. The female may be distinguished from most other species by the acute lateral angle and posterior lobe of its pronotum; from *A. mourei* and *A. boliviensis* by the lack of yellow on its clypeus and by its less finely

branched mesoscutal pubescence; from *A. lanosus* by its finer genal striae and its dark metallic blue-green head and mesosoma.

DESCRIPTION. Female as in *A. mourei* but head and mesosoma dark metallic blue to blue-green; clypeus lacking yellow; pubescence on meso- and metanotum less dense and woolly; tegulae dark brown; metasomal terga often with dark brown bands centrally.

Agapostemon hispaniolicus n. sp.

This species is named for the island of Hispaniola where it occurs.

The male holotype is labeled, "Port-au-Prince/& vic., Haiti/3-X 1934/ Darlington." The allotype is labeled, "Manneville/Haiti/Nov 16-17, '34/ Darlington." The types in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

DISTRIBUTION. In addition to the holotype and allotype, I have seen specimens from Santo Domingo (2 ♀) and Samana (1 ♂, June) in the Dominican Republic; and from La Moriniere (1 ♀, March, 125 ft.) and Port au Prince (1 ♀, April, 300 ft.; 1 ♂) in Haiti.

DIAGNOSIS. The male may be distinguished from other West Indian species, except *A. viridulus* and *A. obscuratus*, by its black metasomal terga and toothed hind femora; from *A. obscuratus* by its bright metallic blue-green head and mesosoma; and from *A. viridulus* by the contiguous punctures on its mesoscutum. The female may be distinguished from other West Indian species, except *A. viridulus* and *A. swainsonae*, by its bright green head and mesosoma and black metasomal terga; from *A. viridulus* and *A. swainsonae* by the finer sculpturing of its interocular area.

DESCRIPTION

MALE (Figs. 115-116, 148)

As in *A. viridulus* but with slightly finer and denser sculpturing; with slightly narrower apical groove on basal ridge of basitarsus; and with shallower and more numerous longitudinal grooves laterally on gonocoxa.

FEMALE (Figs. 37-38)

As in *A. viridulus* but bluer, smaller, and more finely sculptured, clypeal area not as elongate, and with narrower distal keel on labrum.

Agapostemon inca n. sp.

This species is named for the Indians of the Quechuan tribe inhabiting Peru.

The male holotype and one male paratype are labeled, "Hda San Juan/ Col Perene Peru/ 16 June 1920/ Cornell Univ. Exp.// Cornell Univ. Ex-/ pedition Lot 607/ Sub 95." The above two specimens are in the collection of Cornell Univ., Ithaca, N.Y. The only other specimen I have seen is a

male (paratype) in the American Museum of Natural History labeled, "PERU: Montenegro/ Bagua, Amazonas/ Sept. 29-Oct. 2, 1963/ 350m. Wygodzinsky."

Diagnosis. The male may be distinguished from those of most other species by the presence of a medial "button" at the base of its last visible (6th) sternum. This sternal "button" is much longer and broader than that of the closely related *A. mourei* (Figs. 139-140), and the hind femur, tibia and basitarsus are more slender than those of *A. mourei* (Figs. 167-168). *Agapostemon inca* may be distinguished from the related *A. intermedius, A. boliviensis* and *A. lanosus* by the larger and differently shaped medial plate of its gonostylus (Figs. 175, 177 A-B, 192).

Variation. The general appearance of the males differs strikingly because the black markings of the appendages and metasoma may be replaced by pale amber markings.

Description

male (Figs. 140, 168, 175, 218)

As in *A. mourei* but with head and mesosoma dark coppery green; antenna dark brown to black with yellow spot at base of lower side of scape; mesosoma with slightly finer punctures and less coarse rugae; tegula brown to brown-black, nearly obscuring anterior, submarginal, yellow crescent; fore leg yellow with coxa brown, trochanter brown but for anterior yellow spot, and brown on posterior of femur and tibia; middle leg brown with yellow spot on anterior of trochanter, yellow streak on anterior of femur, and small yellow spot anteriorly at either end of tibia; hind leg (Fig. 168) more slender, and dark brown with antero-dorsal yellow patch on femur; metasomal sterna brown with yellow on sterna 2-3; proximo-medial projection, or "button," on sternum 6 (Fig. 140) very broad, base with proximal portion wider than distal portion; genitalia (Figs. 175, 218).

Agapostemon insularis n. sp.

The name of this species refers to its island distribution.

I have seen four specimens (3 ♂, 1 ♀) from the island of Hispaniola. The female holotype and the allotype are labeled "Aux Cayes, Haiti/Mch. 15-20, '22/F. 4644." The two male paratypes are from Carrefour, Haiti (April) and the San Francisco Mts., Dominican Republic (Sept.). The types are in the American Museum of Natural History, New York.

Diagnosis. The male may be distinguished from other West Indian species, except *A. jamaicensis* and *A. poeyi,* by its medial metallic tints on metasomal tergum 3; from *A. jamaicensis* and *A. poeyi* by its lack of postero-lateral metallic tints on metasomal tergum 1. The female may be distinguished from other West Indian species, except *A. poeyi,* by its conspicuous

medial metallic green tints on metasomal sterna 3-4; and from *A. poeyi* by its finely punctate mesoscutellum.

DESCRIPTION

MALE

General coloration of head and mesosoma bright metallic green to blue-green, metasoma brown with yellow bands and tinted with green posteriorly. **Head:** as in *A. viequesensis*. **Mesosoma:** as in *A. viequesensis* but with sculpturing slightly finer, pronotum with lateral angle and posterior lobe both slightly more angular and with fewer postero-lateral carinulae, and tegula with metallic green tints slightly more extensive. **Metasoma:** (21) Terga as in *A. columbi* but with conspicuous metallic tints on tergum 3; pygidium rounded apically as in *A. viequesensis*. (22) *Sterna* as in *A. viequesensis*. (23) *Genitalia* as in *A. poeyi* but with apex of apical stylus on gonostylus slightly smaller (much closer to that of *A. poeyi* than that of *A. viequesensis*).

FEMALE

General coloration of head, mesosoma and metasoma bright metallic greenish blue. **Head:** pubescence as in *A. viequesensis*. (1-4) *Labrum, clypeus, interocular area* and *vertex* as in *A. viequesensis*. (5) *Gena* much more coarsely carinate than that of *A. viequesensis* but not quite as coarse as in *A. poeyi*. (6) *Malar area* absent. (7-8) *Mandible* and *antenna* as in *A. poeyi*. **Mesosoma:** pubescence as in *A. viequesensis* but slightly more fuliginous on mesonotum and metanotum. (9) *Pronotum* as in *A. viequesensis* but with lateral angle and posterior lobe both more angular and with fewer and coarser (not as coarse as in *A. poeyi*) horizontal carinae postero-laterally. (10-12) *Mesoscutum, mesoscutellum* and *metanotum* as in *A. viequesensis*. (13-14) *Mesepisternum* and *metepisternum* as in *A. viequesensis* but with sculpturing very slightly coarser. (15) *Propodeum* as in *A. poeyi* but with finer sculpturing (not quite as fine as in *A. viequesensis*). (16-17) *Wing* and *tegula* as in *A. viequesensis* but tegula darker with metallic tints more extensive. (18-20) *Fore, middle* and *hind legs* dark brown, coxae with strong metallic tints. Pubescence dark amber to brown, scopal hairs white. **Metasoma:** as in *A. viequesensis* but with terga wholly metallic, and sterna 3-4 with strong metallic tints.

Agapostemon intermedius n. sp.

The name refers to the phenotype of this species which is intermediate between that of *A. semimelleus* and that of *A. heterurus*.

The male holotype, the allotype, and the 28 paratypes (4 ♂, 24 ♀) are all from Costa Rica: Gromaco, 34 km southeast of Potrero Grande, on the

Río Coto Brus, southern Puntarenas Province, 21 July 1963, 1,000 ft. (C. D. Michener and W. Kerfoot) and are in the Snow Entomological Museum at the University of Kansas.

Distribution. In addition to the types I have seen specimens from the following localities: Turrialba (2 ♂, 8 July; 1 ♂, 31 July; 1 ♂, 1 Aug.; 1 ♂, 3 Aug.; 1 ♂, 10 Aug.; 1 ♂, 16 Aug.; 2 ♂, 28 Aug.; 1 ♀, 12 Sept.), 4.5 mi. SW Cartago (1 ♀, 3 July) and Pozo Azul at the confluence of Ríos Parrita and Candelaria (1 ♀, 9 Dec.), Costa Rica; 10 miles east of Cumaná, Venezuela (2 ♀, 13 March); Macas, Río Upano (1 ♂, 25 Jan.) and Pichilingue, Los Ríos (5 ♀, 2 Feb.), Ecuador; Monson Valley, Tingo Maria, Peru (1 ♂, 2 Nov.; 2 ♂, 21 Nov.; 3 ♂, 29 Nov.).

Diagnosis. The male is easily distinguished from all other North and Central American *Agapostemon* by its medial "button" (flattened process resembling human tongue and attached to sternum in much the same way as human tongue is attached to floor of mouth) at the base of the last visible (6th) sternum (Fig. 136), and from the South American *Agapostemon* with similar "buttons" on sternum 6 by the low basal ridge and inconspicuous apical groove ventrally on its slender basitarsus (Fig. 151). The female may be distinguished from the other North and Central American species of *Agapostemon* by the basal yellowish bands on its metasomal terga 2-5 (may be obscured by overlapping terga posteriorly), and from South American species with yellow metasomal bands by its bright metallic green or coppery head and mesosoma and the unbroken yellow band on its clypeus (the yellow-banded South American females have only faint metallic tints and nearly always have the yellow clypeal band broken medially).

Variation. The coloration of females of this species varies considerably. While the female head and mesosoma are usually bright metallic green with amber and fuliginous pubescence, I have collected a female from Turrialba, Costa Rica, with bright coppery head and mesosoma and with fulvus pubescence. At first I was inclined to regard it as a separate species but the lack of morphological differences, and the slightly fulvus pubescence of the otherwise typical males from Turrialba, together with the similar pattern of variation in the sympatric *A. leunculus,* lead me to regard these differences as geographic variation.

The color of the yellow-banded metasomal terga of females varies from pale amber (Gromaco and Pozo Azul, Costa Rica; Cumaná, Venezuela; and Pichilingue, Ecuador) to brown-black (Turrialba, Costa Rica; Cumaná, Venezuela; and Pichilingue, Ecuador). Although it is difficult to assess such variation on the basis of so few specimens it appears that the color of the yellow-banded metasomal terga varies both within and among populations as does that of the North American *A. melliventris.*

DESCRIPTION

MALE (Figs. 81-82, 136, 151, 192, 214)

General coloration of head and mesosoma bright metallic green, metasoma banded with black and yellow. **Head** (Figs. 81-82): with pubescence golden to fulvus on interocular area and vertex, becoming creamy on gena. (1) *Labrum* as in *A. texanus* but with apical portion much shorter and more acute at apex. (2) *Clypeus* with large, scattered, shallow punctures on lower (yellow) ½-⅔, becoming contiguous on upper (green) ⅓-½. (3) *Interocular area* with small to moderately small, deep, contiguous punctures below ocelli, becoming shallower and medium-sized at level of antennal sockets and still shallower below antennae; supraclypeal protuberance with large contiguous moderately deep punctures. Pubescence between antennal sockets ½-⅔ as long as scape, becoming shorter laterally, dorsally and ventrally and subtomentose ventro-laterally. (4) *Vertex* with small, deep, contiguous punctures anteriorly and laterally, becoming shallower and slightly larger between ocelli and transversely carinate posteriorly. (5) *Gena* with parallel, subcontiguous, short (often very weak) carinae extending dorsolaterally from antero-ventral margin. Pubescence about as long as scape postero-medially, becoming shorter anteriorly, laterally and dorsally. (6) *Malar area* yellow, very short, and with minute, appressed hairs. (7) *Mandible* yellow with apical ⅓ ferruginous to amber. (8) *Antenna* brown to brown-black above, scape yellow below, pedicel and flagellum yellowish to amber below. **Mesosoma:** pubescence creamy or yellowish becoming golden to fulvus on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe acutely pointed, lateral angle projecting anterolaterally; with conspicuous sharp carina extending postero-ventrally from apex of lateral angle; with weak irregular rugae postero-laterally. Pubescence above lateral angle and posterior lobe golden to fulvus, yellowish to creamy below. (10) *Mesoscutum* with large conspicuous flange laterally on anterior margin extending antero-dorsally; punctures small, very deep and contiguous, becoming rugose antero-laterally. (11) *Mesoscutellum* with medial punctures like those of mesoscutum, becoming slightly larger and less dense laterally; relatively shiny area with widely separated punctures on each side of midline. (12) *Metanotum* coarsely punctate to rugose medially, becoming moderately coarsely rugose laterally. (13) *Mesepisternum* moderately coarsely rugose anteriorly, becoming finely rugose posteriorly. (14) *Metepisternum* moderately finely rugose with horizontal rugae longer and slightly more prominent than other rugae, or with irregular horizontal carinae. (15) *Propodeum* with propodeal carina usually strong and conspicuous; propodeal shield very coarsely and deeply punctate to very coarsely rugose; dorsal area coarsely and very deeply rugose anteriorly and medially, becoming deeply and moderately rugose to coarsely punctate laterally; lateral area with small

and very deep subcontiguous punctures anteriorly and centrally, becoming coarsely rugose adjacent to propodeal carina. (16) *Wing* hyaline or nearly hyaline, veins dark brown. (17) *Tegula* pale to dark transparent amber with broad submarginal yellow band anteriorly (partially obscured by pubescence) and amber to dark brown on proximal margin. (18) *Fore leg* yellow with brown streaks posteriorly on femur and tibia. (19) *Middle leg* yellow with coxa brown and with brown postero-dorsally on tibia and postero-dorsally at apex of femur (also present posteriorly on trochanter of some specimens). (20) *Hind leg* (Fig. 151) yellow with upper ½ of coxa brown and tinted metallic green; with trochanter brown basally, becoming amber apically; with brown apically on femur and antero-dorsally on tibia.

Metasoma: (21) *Terga* 2-6 dark brown to brown-black on posterior ½ and yellow on anterior ½ (often partially concealed by overlap), tergum 1 dark brown to brown-black with broad yellow band antero-dorsally (centrally); very conspicuously punctate with subcontiguous punctures largest on tergum 1, becoming progressively smaller on posterior terga. Pubescence golden to fulvus anteriorly on tergum 1, laterally on terga 1-7 and dorsally on terga 5-7; very short dorsally on terga 1-4, golden to fulvus on yellow bands and dark brown to brown-black on dark bands. (22) *Sterna* yellow with brown on sternum 1 and with transverse bands on posterior margins of sterna 2-5 narrowest on sternum 2, becoming progressively wider (especially medially) posteriorly; sternum 6 with proximo-medial projection, or "button," in form of human tongue (Fig. 136); pubescence limited to scattered, moderately long, fulvus to golden hairs on exposed areas. (23) *Genitalia* (Figs. 192, 214) with ventral lobes very short and with a brush of large stiff hairs.

FEMALE (Figs. 47-48)

General coloration of head and mesosoma bright metallic green or coppery, metasoma pale amber to black and with yellow bands. **Head** (Figs. 47-48): pubescence golden to fulvus, becoming creamy to golden on gena. (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with large scattered punctures on lower ½, becoming subcontiguous on upper ½. (3) *Interocular area* with small, moderately deep, contiguous punctures below ocelli, becoming rugose from just above antennal sockets to lower margin; supraclypeal protuberance with medium sized punctures separated by nearly twice their diameters and with short, inconspicuous horizontal rugae. (4) *Vertex* with small, moderately deep, contiguous punctures anteriorly and laterally, becoming subcontiguous between ocelli and transversely carinate posteriorly. (5) *Gena* with fine, contiguous, parallel carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* amber, very short to absent. (7) *Mandible* yellow, becoming dark amber or ferruginous on apical ⅓.

(8) *Antenna* dark brown to brown-black with underside of flagellum amber. **Mesosoma:** pubescence creamy to golden, becoming golden (with large scattered hairs dark) to fulvus (with large scattered hairs pale) on mesonotum and metanotum. (9) *Pronotum* as in ♂ but with weak carina extending from lateral angle to posterior lobe. (10) *Mesoscutum* as in ♂ but with most punctures slightly smaller and shallower (large scattered hairs in large punctures). (11) *Mesoscutellum* with sculpturing like that of mesoscutum but with small punctures slightly shallower. (12) *Metanotum* moderately finely rugose. (13) *Mesepisternum* as in ♂ but with sculpturing slightly more coarse. (14) *Metepisternum* horizontally carinulate with interconnecting rugae. (15) *Propodeum* with strong propodeal carina; propodeal shield with conspicuous carinae extending dorso-laterally from medial groove and with fine rugae between conspicuous carinae; dorsal area coarsely and extremely deeply rugose anteriorly and medially, becoming moderately deeply and less coarsely rugose laterally; lateral area horizontally carinulate with small scattered punctures anteriorly becoming very coarsely and horizontally carinate posteriorly. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but slightly darker. (18) *Fore leg* with dark brown on coxa and trochanter; femur dark brown, becoming yellow anteriorly and dorsally on apical ⅓; tibia and tarsus yellowish to pale amber anteriorly, becoming brown posteriorly. Pubescence creamy on coxa, trochanter and femur; golden on tibia and tarsus. (19) *Middle leg* dark brown, becoming pale amber to yellowish anteriorly and dorsally on apical ¼ of femur and at base of tibia; pubescence creamy on coxa and trochanter, becoming golden on femur, tibia and tarsus, and dark brown dorsally on tibia and tarsus. (20) *Hind leg* dark brown to pale brown with metallic green dorsally on coxa. Pubescence creamy on coxa, trochanter and femur; golden ventrally and dark brown to brown-black dorsally on tibia and tarsus. **Metasoma:** (21) *Terga* 2-5 pale amber to black, with yellow band on basal ⅓ of each (may be partially obscured by overlap); tergum 1 pale amber to black with inconspicuous pale spot dorso-laterally. Punctures small, separated by about ½ their diameters. Pubescence moderately short, amber to brown dorsally on terga 1-4 but with sparsely scattered longer and darker hairs increasing in size and abundance posteriorly from tergum 1; medium length, creamy to amber anteriorly on tergum 1 and laterally on terga 1-4; moderately long, dense and dark brown to black on terga 5-6. (22) *Sterna* dark brown on specimens with brown to brown-black on tergum 1, but sterna 1-3 and base of sternum 4 amber on specimens with tergum 1 amber; metallic tints basally on sternum 1. Long amber pubescence scattered on exposed areas.

Agapostemon jamaicensis n. sp.

This species is named for the island where it occurs.

I have seen a single male specimen labeled, "Moneage, Jamaica./Sept. 14,

1917 (497)/Harold Morrison." The holotype is in the United States National Museum, Washington, D.C.

Diagnosis. The male may be distinguished from other West Indian species, except *A. poeyi* and *A. insularis,* by its posterior metasomal terga strongly tinted with metallic green medially and by its brown eyes and translucent amber to brown pterostigma; from *A. insularis* by its metallic green tints postero-laterally on metasomal tergum 1; and from *A. poeyi* by its more inflated hind femur and tibia.

Description

male (Fig. 146)

General coloration of head and mesosoma bright metallic blue-green, metasoma dark brown banded with yellow anteriorly, becoming bright metallic green posteriorly. **Head:** as in *A. viequesensis* but with sculpturing very slightly coarser and with pubescence pale amber. **Mesosoma:** pubescence as in *A. viequesensis.* (9) *Pronotum* as in *A. viequesensis* but with lateral angle and posterior lobe slightly more angular. (10-12) *Mesoscutum, mesoscutellum* and *metanotum* as in *A. viequesensis.* (13-14) *Mesepisternum* and *metepisternum* with sculpturing coarser than in *A. viequesensis* but not as coarse as in *A. poeyi.* (15) *Propodeum* as in *A. poeyi* females but with sculpturing slightly finer and antero-lateral area with large punctures replacing carinae. (16-19) *Wing, tegula, fore* and *middle legs* as in *A. viequesensis.* (20) *Hind leg* as in *A. viequesensis* but with femur and tibia more inflated, apical groove on basitarsus broader and convex centrally, and basal ridge more prominent with broad flat area on apical portion (Fig. 146). **Metasoma:** (21) *Terga* as in *A. viequesensis* but slightly darker and with bright metallic green replacing brown band completely on tergum 4 and partially on terga 1-3 and 5-6. (22) *Sterna* as in *A. viequesensis* but dark amber. (23) *Genitalia* as in *A. poeyi* but with apex of apical stylus of gonostylus more slender than that of *A. poeyi* (not as slender as *A. viequesensis*).

Agapostemon kohliellus (Vachal)

Halictus (Agapostemon) kohliellus Vachal 1903. Type ♀, Naturhistorisches Museum, Vienna.

I have examined the type of *H. kohliellus* and the locality label is illegible. This species is atypical of the genus inasmuch as the labrum of the female is trilobed (Fig. 31). For the present study it is included in *Agapostemon* because it is phenetically closer to this genus than to any other. Ultimately it may be desirable to erect a separate genus for this species.

Distribution. Other than the type, I have seen specimens from Port au Prince (1 ♀, March) and Cul-de-Sac Plain (3 ♂, Dec.) Haiti and from Río Toa Baracoa, Cuba (1 ♂, April).

DIAGNOSIS. The male may be distinguished from all other West Indian species by its truncate clypeus, hind femur lacking tooth, and unique hind basitarsus. The females may be distinguished from all other West Indian species by the yellow band on the clypeus and by the yellow bands on the honey-colored metasoma.

DESCRIPTION

MALE (Figs. 109-110, 141, 191, 212)

General coloration of head and mesosoma metallic green, metasoma yellow with brown bands. **Head** (Figs. 109-110): pubescence white to yellowish on clypeus, interocular area and vertex; white on gena. (1) *Labrum* yellow, with apical margin transparent; apex truncate to very slightly bilobed, basal ½ without medial depression on transverse basal ridge; labral surface shiny and impunctate with row of small, simple submarginal setae. (2) *Clypeus* yellow with metallic green on upper margin, truncate, but not nearly as much as in *A. nasutus* (Figs. 85-87); flattened lower portion with several small shallow punctures and nearly glabrous, narrow upper portion with shallow scattered punctures and with short sparse pubescence. (3) *Interocular area* with deep, coarse, contiguous punctures above; deeply rugulose around antennal sockets, becoming less deeply rugulose below. Supraclypeal protuberance small but relatively acute, shallowly and coarsely rugose below, weakly rugulose above. Pubescence between antennal sockets about ⅔ as long as scape, becoming slightly shorter dorsally, laterally and ventrally; becoming short appressed tomentum ventro-laterally. (4) *Vertex* with deep, contiguous, medium-sized punctures anteriorly, laterally and between ocelli; becoming rugose posteriorly. Pubescence like that of dorsal portion of interocular area. (5) *Gena* with weak rugae extending postero-dorsally from antero-ventral margin; postero-medial pubescence slightly longer than that between antennal sockets, becoming shorter anteriorly, laterally and dorsally. (6) *Malar area* absent. (7) *Mandible* yellow, ferruginous on apical ⅓. Row of hairs on postero-ventral margin only ⅓ as long distally as proximally. (8) *Antenna* brown above, but scape with yellow on basal ½ of upper surface; scape and pedicel yellow below, flagellum amber below. **Mesosoma:** pubescence white, yellowish on mesonotum and metanotum. (9) *Propodeum* with lateral angle and posterior lobe rounded; sculpturing weak and inconspicuous. (10) *Mesoscutum* with deep, small, contiguous punctures becoming rugose antero-laterally. (11) *Mesoscutellum* with small, deep punctures separated by at least their diameters, becoming rugose laterally. (12) *Metanotum* shallowly rugose with small, deep punctures more abundant than those of mesoscutellum. (13) *Mesepisternum* finely rugulose anteriorly, becoming very finely rugulose posteriorly. (14) *Metepisternum* horizontally carinulate. (15) *Propodeum* rounded posteriorly

with propodeal carina absent; small, deep punctures laterally separated by at least their own diameters, becoming rugulose or contiguously punctate postero-dorsally; propodeal shield shallowly rugulose. (16) *Wing* transparent; veins and pterostigma dark brown, radius almost black. (17) *Tegula* pale transparent honey-colored with yellow on basal margin and with yellow band almost reaching distal margin. (18-19) *Fore* and *middle legs* yellow with coxae metallic green. (20) *Hind leg* (Fig. 141) yellow with trochanter brownish, brown apically on dorsal surface of femur and amber on all but ventral surface of tibia, and with coxa metallic green; femur without tooth; femur and tibia moderately inflated; basitarsus broad but flat with basal ridge narrow and gently curved apically; basitarsus lacking apical groove. **Metasoma:** (21) *Terga.* Tergum 1 yellow, amber anteriorly and brown apically; terga 2-6 with basal yellow band and apical brown band of equal width; tergum 7 amber. Pubescence minute and inconspicuous dorsally, amber on yellow bands, and black on brown bands; long brown hairs dorsally on terga 5-7; long pale hairs ventro-laterally on terga 4-6 and anteriorly on tergum 1. (22) *Sterna* amber with white hairs on exposed areas. (23) *Genitalia* (Figs. 191, 212), ventral lobe short with long brush of hairs on short inner portion.

female (Figs. 31-32)

General coloration of head and mesosoma bright metallic green, metasoma honey-colored with yellow bands. **Head** (Figs. 31-32): with short white pubescence. (1) *Labrum* (Figs. 31A-B) with acute lateral lobes on apical ½. (2) *Clypeus* yellow below, green above; yellow portion shiny, sparsely punctate, green portion with medium-sized deep, contiguous punctures. (3) *Interocular area* rugulose, becoming finely and deeply punctate above; supraclypeal protuberance low and gently rounded with medium-sized punctures separated by their own diameters and with numerous horizontal rugae; pubescence between antennal sockets only about ⅓ as long as scape. (4) *Vertex* with fine, deep, contiguous punctures anteriorly, becoming smaller, shallower and subcontiguous laterally and faintly rugulose posteriorly; area between ocelli shiny with small scattered punctures. (5) *Gena* with fine, contiguous rugulae extending postero-dorsally from antero-ventral margin; pubescence postero-medially about 1.5 × as long as pubescence between antennal sockets and becoming shorter anteriorly, laterally and dorsally. (6) *Malar area* absent. (7) *Mandible* yellow with apical ⅓ ferruginous; single row of hairs on postero-ventral margin long basally, becoming ⅓ as long distally. (8) *Antenna* brown, flagellum yellowish to amber below. **Mesosoma:** short white to yellowish pubescence. (9) *Pronotum* with lateral angle and posterior lobe rounded; sculpturing very fine, weak and irregularly rugulose ventro-laterally, becoming smooth dorso-

medially. (10) *Mesoscutum* with small contiguous punctures, becoming faintly rugulose antero-laterally. (11) *Mesoscutellum* shiny, with scattered large punctures and more numerous very small punctures. (12) *Metanotum* sparsely punctate, irregularly and transversely rugulose. (13) *Mesepisternum* with shallow, fine rugae anteriorly, becoming much finer and transversely rugulose to carinulate posteriorly. (14) *Metepisternum* with shallow, regular transverse carinulae. (15) *Propodeum* with distinct but weak propodeal carina; very fine, regular, horizontal carinulae laterally and on propodeal shield; dorsal area with very fine carinulae extending postero-laterally from anterior margin. (16-17) *Wing* and *tegula* as in ♂. (18-20) *Fore, middle* and *hind legs* yellowish to amber with white to yellowish pubescence becoming fuliginous dorsally on middle and hind tibiae. **Metasoma:** (21) *Terga* amber to pale brown with yellow bands basally on terga 2-5; tergum 1 may have pale yellow band anteriorly on dorsal portion interrupted medially; pubescence as in ♂. (22) *Sterna* amber to brown with long white hairs scattered on exposed areas.

Agapostemon lanosus n. sp.

The name of the species refers to the woolly appearance of the mesoscutal pubescence.

The male holotype and the allotype are labeled, "PERU:/ Monson Valley/ Tingo Maria/ XI-21-1954// E. I. Schlinger/ &E. S. Ross collectors." The two male paratypes were collected by Ross and Schlinger from the same locality on "29-XI-1954" and "XII-23-1954." At present, these types are the only known specimens and they are in the California Academy of Sciences, San Francisco.

DIAGNOSIS. The male may be distinguished from most other species by the presence of a medial "button" at the base of its last visible (6th) sternum (Fig. 138). It may be distinguished from other species with sternal "buttons" by the presence of 2-3 long (about twice the length of adjacent setae), thickened, apically hooked setae laterally on the posterior margin of the antepenultimate visible (4th) sternum.

The female may be distinguished from most other species by the acute lateral angle and posterior lobe of its pronotum and by the dense woolly pubescence of its mesoscutum; from *A. mourei* and *A. boliviensis* by the lack of yellow on its clypeus, by its less finely branched mesoscutal pubescence and by its coarser genal sculpturing; from *A. heterurus* by the parallel striae dorsally on its pronotum and by the coppery luster of its head and mesosoma.

VARIATION. The general appearance of the males varies strikingly because the black markings of the appendages and metasoma may be replaced by pale amber markings.

Description

male (Figs. 138, 169, 177B, 216)

As in *A. mourei* but with head and mesosoma bright coppery green; antenna dark brown to black with scape yellow below; mesoscutellum with punctures widely scattered in central region; tegula darker amber with anterior, submarginal, yellow crescent partially obscured proximally; fore leg yellow with brown on posterior of coxa, trochanter, femur and tibia and anteriorly at base of coxa; hind basitarsus (Fig. 169) yellow with dark brown to black on ventral carina; metasomal sterna dark brown with yellow on sterna 2-3; sternum 6 (Fig. 138) with proximo-medial projection, or "button," with each lateral flange slightly less than ½ width of base (as measured on transverse section through widest part of "button"); genitalia (Figs. 177B, 216).

female

As in *A. mourei* but clypeus without yellow band; gena with deeper striae; meso- and metanotum with pubescence darker and slightly less woolly; propodeum dorsally with coarse, deep striae extending posterolaterally from anterior margin; metasoma dark brown with yellowish amber on tergum 1 and proximo-laterally on terga 2-5.

Agapostemon leunculus Vachal

Agapostemon leunculus Vachal 1903. **Lectotype** ♀, Muséum National D'Histoire Naturelle, Paris.

Agapostemon vulpicolor Crawford 1906 **(new synonymy).** Type ♀, U.S. National Museum.

Agapostemon nasutus var. *ater* Friese 1916 **(new synonymy).** Type ♀, whereabouts unknown.

From the 30 syntypes of *Agapostemon leunculus* in the Paris Museum, I have designated a female as lectoholotype. I have seen the type of *A. vulpicolor* but not that of *A. nasutus ater*. As noted by Michener (1954), *A. nasutus ater* is not conspecific with *A. nasutus*. I have seen a female "Typus" (not a type, but identified by Friese) of *A. nasutus ater* from the U.S. National Museum labeled, "Costa Rica,/San José,/1903." Friese did not describe the male, probably because he was expecting to find something with the "hog-nosed" aspect of *A. nasutus*. The only difference between *A. leunculus* and *A. nasutus ater* is the coloration of the pubescence and integument of the head and the dorsal surface of the thorax. I have not found any differences among the males that can be correlated with the variation among females. Because I have seen females intermediate in coloration (see discussion of variation) I am considering the difference between *A. leunculus* and *A. nasutus ater* as local variation.

Distribution. *Agapostemon leunculus* is found in Mexico exclusive of the central plateau, as far north along the eastern coast as ten miles southwest of Pharr, Texas (1 ♀ collected by C. D. Michener) and as far north

along the western coast as Rosario, Sinaloa. It has been collected in the mountainous regions of southern Mexico but has not been taken on the Yucatan Peninsula. It has also been collected in the mountains of El Salvador, Honduras, Costa Rica, Panama, Colombia and Ecuador (Fig. 5).

Although information on altitudinal distribution is scant, this species has not been found at low altitudes (less than 1,000 m) in the hot tropics. It has been collected from 32 m (105 ft.) at Rosario, Sinaloa, Mexico, up to 7,100 ft. (2,164 m) near Nochixtlán, Oaxaca, Mexico; from 3,300 ft. (1,006 m) at Santiago de Puriscal, Costa Rica, up to 9,000 ft. (2,743 m) on Volcan Irazú, Costa Rica; 7,800 ft. (2,377 m) at Popayan, Colombia, and 2,800 m (9,184 ft.) at Calacali, Ecuador. *A. leunculus* has been collected in February and October in Ecuador; February in Colombia; every month but January, March, June and November in Central America; every month but January and November in Mexico; and on March 31 near Pharr, Texas. Undoubtedly this bee is more widely distributed altitudinally and seasonally than is indicated by these records. I have seen fewer than 300 specimens, and this sample is probably biased because bee collectors seldom work as high as 3,000 m and because most of the specimens were collected by North Americans, who seldom have an opportunity to collect from October through May.

DIAGNOSIS. The male may be differentiated from males of many other species by its slender, untoothed hind femora and rounded lateral pronotal angle; from *A. nasutus* by its normal clypeal region; from *A. rhopalocera* by its normal antennae; from *A. peninsularis* and *A. mexicanus* by its lack of enlarged subapical hairs on metasomal sternum 4; and from *A. melliventris* by the black on the basal portion of its metasomal tergum 1. The female may be distinguished from other species with black metasoma and green or coppery head and mesosoma by the prominent carina extending postero-ventrally from the rounded lateral angle of its pronotum.

VARIATION. The coloration of the head and dorsal mesosomal region, as well as the pubescence thereon, is quite variable in females of this species. Most of the females are metallic green on the head and thorax. Some of the females from Costa Rica (Volcan Irazú, San José, Cartago and San Mateo) have reddish or coppery integument on the head and the dorsal mesosomal area. The pubescence on these areas is orange. Although nowhere else so extreme, I have seen females from Mexico (e.g., Orizaba, Vera Cruz; Ajijic, Jalisco; Tehuacan, Puebla; and near Oaxaca, Oaxaca) with orange pubescence and with coppery tints on the head and the dorsal mesosomal area. In still other areas (e.g., near Ciudad del Maiz and San Luis Potosí) the integument is green but the pubescence orange. In those regions where the orange of the pubescence and the coppery color is most pronounced, the yellow band on the clypeus of females is often reduced or absent. As these regions are relatively cool and wet, it is not surprising that the females are

more darkly pigmented. The pigmentation of the males is correlated with that of the females. Those males with enlarged black or brown markings are found with the darker females. As in the females, intergrades may be found between the lightest and darkest males. It is the presnce of color intergrades and the lack of structural differences that lead me to synonymize *A. leunculus* and *A. nasutus ater*. Some of the females from Costa Rica, Colombia and Ecuador have fuliginous pubescence on the head and dorsal mesosomal regions, but sympatric intermediates exist for this condition also. The tegulae of those females with orange or fuliginous pubescence are often dark brown to black, unlike the more common yellow and transparent tegulae of females from warmer, drier areas.

Description

male (Figs. 83-84, 143, 193, 211)

General coloration of head and mesosoma metallic green, metasoma with black and yellow bands. **Head** (Figs. 83-84): (1) *Labrum* as in *A. texanus* but more acute apically. (2) *Clypeus* with small scattered punctures on yellow portion, larger and deeper scattered punctures on green portion; scattered yellowish hairs directed ventrally. (3) *Interocular area* with punctures above antennal sockets contiguous, deep and nearly rugose; coarsely and shallowly punctate at level of antennal sockets becoming coarsely, shallowly and irregularly rugose below; supraclypeal protuberance with coarse, contiguous punctures; pubescence pale amber. (4) *Vertex* with fine, contiguous punctures becoming coarse posteriorly; pubescence pale amber. (5) *Gena* with sparse, shallow carinae extending postero-dorsally from antero-ventral margin; pubescence dense, white, longest posteriorly. (6-7) *Malar area* and *mandible* as in *A. texanus*. (8) *Antenna* dark brown to black above except basal ½ of scape; yellow to amber below, basal ½ of scape usually yellow. **Mesosoma:** pubescence moderately long, evenly distributed (except pronotum), and whitish to amber. (9) *Pronotum* with weak carina running postero-ventrally from lateral angle; condition of lateral angle and posterior lobe intermediate between *A. nasutus* and *A. texanus*. Pubescence above and between lateral angle and posterior lobe similar to that of mesoscutum; short, white, appressed, inconspicuous pubescence on postero-ventral surface. (10) *Mesoscutum* with punctation as in *A. nasutus* but slightly finer and with rugosity restricted to antero-lateral portions. (11) *Mesoscutellum* with punctures slightly deeper and larger than those of mesoscutum. (12) *Metanotum* coarsely punctate medially to shallowly rugose laterally. (13) *Mesepisternum* with punctation as in *A. nasutus*. (14) *Metepisternum* with predominately horizontal, irregularly anastomosing rugae not as regular as in *A. nasutus*. (15) *Propodeum* coarsely punctate antero-laterally becoming moderately rugose postero-laterally and

very coarsely rugose dorsally; propodeal carina weak, evenly rounded dorsally, sometimes obscured by coarse rugae; propodeal shield very coarsely and irregularly rugose. (16) *Wing* transparent, not darkened apically, radius scarcely darker than other veins. (17) *Tegula* as in *A. nasutus* but transparent brown proximally and with less yellow. (18) *Fore leg* yellow, often with postero-dorsal black streak on any or all segments but tarsus; pubescence as in *A. nasutus* but yellow to amber on tibia and tarsus. (19) *Middle leg* yellow with coxa brown to black, postero-dorsal brown streak on proximal ½ of tibia, and commonly with brown streak on part or entire length of postero-dorsal surface; pubescence like that of fore leg but shorter on coxa, trochanter and femur. (20) *Hind leg* (Fig. 143) coxa metallic green and usually with some yellow on ventral surface; trochanter predominately yellow, brownish dorsally to wholly brown or black; femur with brown dorsally and posteriorly at apex; proximal ½ of tibia with brown streak on dorsal ½ sometimes extending to apex; tarsus yellow to brown; pubescence as in *A. nasutus* but slightly shorter and darker. **Metasoma:** (21) *Terga* shiny; 2-6 with yellow on basal ½, apical ⅔ black; tergum 1 black with yellow band on antero-dorsal surface; tergum 7 yellow basally, pygidial region brown to black; pubescence sparse, simple, moderately long, and white on vertical portion of tergum 1; terga 2-4 with short simple hairs, white on yellow bands and black on dark bands; terga 5-7 with moderately long, stiff, simple, black hairs. (22) *Sterna* 2-5 yellow with brown bands subapically; sternum 1 green basally, apical ½ yellow with amber medial stripe; pubescence white, short and simple. (23) *Genitalia* (Figs. 193, 211) very simple; penis valves broad and without conspicuous prominences; gonostylus elongate with short curved apical stylus and long medial plate of moderate width; ventral lobes notched as in *A. nasutus* but smaller and with smaller notches.

FEMALE (Figs. 45-46, 135)

General coloration of head and mesosoma dark metallic green to blue-green, metasoma shiny black with narrow, inconspicuous basal bands of white tomentum. **Head** (Figs. 45-46): (1-4) *Labrum, clypeus, interocular area* and *vertex* as in *A. nasutus* but with slightly coarser sculpturing and with pubescence white to yellow or fuliginous. (5) *Gena* with deep, coarse, parallel carinae running postero-dorsally from antero-ventral margin irregularly anastomosing on some specimens; pubescence white (never yellow) and shorter than in *A. nasutus*. (6) *Malar area* ferruginous, very short. (7) *Mandible* as in *A. nasutus*. (8) *Antenna* black above, dark brown below, undersides of first two flagellomeres often lighter than others. **Mesosoma:** metallic green, never with yellow spot on posterior lobe of pronotum, as in *A. nasutus*. (9) *Pronotum* (Fig. 135) as in *A. nasutus* but with

prominent carina running postero-ventrally from lateral angle. (10-12) *Mesoscutum, mesoscutellum* and *metanotum* with punctation as in *A. nasutus* but slightly finer and without shiny lateral area on mesoscutellum; pubescence more dense than in *A. nasutus* and white to orange or fuliginous. (13) *Mesepisternum* very coarsely rugose anteriorly to moderately rugose posteriorly; white to yellowish pubescence. (14) *Metepisternum* with moderately coarse horizontal carinae anteriorly, becoming rugose posteriorly; pubescence creamy. (15) *Propodeum* coarsely rugose dorsally and postero-laterally, becoming finely rugose antero-laterally; propodeal carina prominent, strongly curved dorsally and laterally; propodeal shield with irregularly anastomosing carinulae extending laterally from mid-line. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but may also be brown to black. (18) *Fore leg* dark brown, usually with some yellow on antero-apical portion of femur and antero-basal portion of tibia; pubescence yellowish brown ventrally, brown to black dorsally. (19-20) *Middle* and *hind legs* dark brown, with pubescence brown ventrally and black dorsally. **Metasoma:** (21) *Terga* black, shinier than in *A. nasutus*. Narrow basal bands of white tomentum on terga 2-5; long, pale hairs scattered on vertical portion of tergum 1 and lateral margins of terga 2-5; long black hairs on apical half of terga 4-5. (22) *Sterna* black with long pale hairs on exposed areas.

Agapostemon melliventris Cresson

Agapostemon melliventris Cresson 1874 (not 1875). Type ♀, Academy of Natural Sciences, Philadelphia.
Agapostemon fasciatus Crawford 1901 **(new synonymy).** Type ♀, U.S. National Museum.
Halictus (Agapostemon) plurifasciatus Vachal 1903 **(new synonymy).**
Agapostemon digueti Cockerell 1924. Type ♀, California Academy of Sciences, San Francisco.

Cresson described this species as new in two different publications (1874, 1875). Obviously the earlier publication is valid and the latter superfluous.

I have seen the types of *Agapostemon melliventris, A. fasciatus* and *A. digueti* and believe they are conspecific. *Agapostemon fasciatus* Crawford has been considered by most authors to be of subspecific rank because it differs from *A. melliventris sensu stricto* in having females with black metasomal terga. I have accorded it neither subspecific status, because in many areas (cf. Arizona, Fig. 6) it is sympatric with *A. melliventris s.s.*, nor specific status because intermediate forms are too common (cf. discussion of variation).

When Vachal placed *Agapostemon* in the genus *Halictus, Agapostemon fasciatus* became a junior secondary homonym of *Halictus fasciatus* Nylander. Thus Vachal renamed the former *Halictus (Agapostemon) plurifasciatus*. Few workers agreed with Vachal's placement of *Agapostemon* as a subgenus of *Halictus*. If other workers wish to apply a name to this dark color form they should use the epithet proposed by Vachal. Cockerell

(1937a) and Michener (*In* Muesebeck, et al., 1951) believed Crawford's epithet should be used, but according to the International Code of Zoological Nomenclature (anonymous, 1964) secondary homonyms rejected before 1961 cannot be revived (cf. *Agapostemon coloradinus*).

DIAGNOSIS. The male may be distinguished from other species of *Agapostemon* by its yellow metasomal terga with brown to brown-black restricted to narrow subapical bands. The female may be distinguished from other North American species (except *A. nasutus, A. leunculus* and *A. peninsularis*) by the yellow band on the lower margin of its clypeus; from *A. nasutus* by the lack of a yellow spot on the posterior lobe of its pronotum; from *A. leunculus* by its lack of a prominent carina extending postero-ventrally from the lateral angle of the pronotum; and from *A. peninsularis* by its coarser propodeal sculpturing and less dense pubescence. In most females of *A. melliventris* the metasomal terga are pale amber, unlike the black metasomal terga of *A. peninsularis* (and some specimens of *A. melliventris*).

VARIATION. The most striking variation is the color of the metasoma of females (see map, Fig. 6). In females from the central plains of Oklahoma, Kansas, Nebraska and South Dakota, the metasoma is almost always black. From the opposite side of the range, in females from Baja California and Sonora, it is more commonly black than amber. In the remaining portion of the range the female metasoma is usually amber, but a few females with the metasoma black or dark brown may be found in these regions. I have seen specimens intermediate with respect to color of abdomen in all areas, but they are rare in the central plains. The amount of yellow on the clypeus and scape is positively correlated with the paleness of the metasoma, those specimens from the central plains having a narrow band of yellow on the clypeus and little or no yellow on the scape.

There is no variation in the color or color pattern of males corresponding to that of females. The size and darkness of the brown regions on the metasoma, legs and antennae varies slightly within, but not among, populations.

One of the most obvious variables in the phenotype is size. As shown in Figures 93-94, the linear dimensions of larger specimens may be nearly twice those of smaller specimens collected at the same time and place. This size variation is somewhat greater among males than among females and does not appear to be influenced by geographic factors.

DESCRIPTION

MALE (Figs. 92-94, 155, 188, 203)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma yellow with narrow brown bands; all pubescence white.

Head (Figs. 92-94): (1) *Labrum* as in *A. texanus* but with transparent distal margin slightly wider. (2) *Clypeus* with medium-sized punctures separated by about their diameters below, nearly contiguous above. (3) *Interocular area* with medium-sized, moderately deep, contiguous punctures becoming minute, shallow and sub-contiguous ventro-laterally. (4) *Vertex* with medium-sized, moderately deep, contiguous punctures anteriorly, becoming slightly smaller and shallower laterally, and rugulose posteriorly and between ocelli. (5) *Gena* with very weak, short, parallel carinulae extending postero-dorsally from antero-ventral margin. (6) *Malar area* yellow; short. (7) *Mandible* yellow with distal third ferruginous to amber. (8) *Antenna* with scape yellow (small brown spot apically on upper side on some specimens); pedicel dark brown above, yellow below; flagellum dark brown above (yellow at apex of last flagellomere) and yellow to pale amber below. **Mesosoma:** (9) *Pronotum* with lateral angle and posterior lobe rounded; low rounded vertical ridge below lateral angle and faint, parallel, horizontal carinae below posterior lobe. (10) *Mesoscutum* with moderately fine, moderately deep, contiguous punctures becoming rugose antero-laterally. (11) *Mesoscutellum* with punctures like those of mesoscutum but slightly less dense and sometimes subcontiguous laterally. (12-13) *Metanotum* and *mesepisternum* moderately finely rugose. (14) *Metepisternum* with sculpturing as in mesepisternum but slightly coarser and horizontal. (15) *Propodeum* with propodeal carina moderately weak; propodeal shield coarsely but shallowly rugose; dorsal area coarsely and moderately deeply rugose; lateral area with moderately coarse rugae postero-dorsally, becoming moderately finely rugose antero-ventrally. (16) *Wing* hyaline; radial vein brown, other veins and pterostigma pale amber. (17) *Tegula* colorless and transparent with opaque yellow band submarginal anteriorly, marginal basally and posteriorly. (18-19) *Fore* and *middle legs* yellow with coxae bright metallic green. (20) *Hind leg* (Fig. 155) like fore and middle legs but with brown spot distally on dorsal surface of femur and basally on dorsal surface of tibia; femur without tooth and basitarsus without apical groove or basal ridge. **Metasoma:** (21) *Terga* yellow with narrow, subapical, brown bands and with apical ¼-⅓ transparent, pale amber; tergum 1 with anterior surface very pale amber to yellow; tergum 7 with pygidium pale amber. Short appressed pubescence dorsally becoming moderately long anteriorly, posteriorly and laterally. (22) *Sterna* yellow with faint metallic tints basally on sternum 1; narrow brown bands subapically on sterna 2-4; broad brown band subapically on sternum 5; and sternum 6 largely brown, with pale amber to yellow disto-laterally; moderately short to moderately long scattered hairs on exposed areas. (23) *Genitalia* (Figs. 188, 203) with medium-sized and slightly elongate ventral lobe on gonocoxite fringed with hairs and with short hairs rather dense on posterior surface.

FEMALE (Figs. 61-62)

General coloration of head and mesosoma bright metallic green to blue-green; metasoma pale amber to black and with broad bands of white tomentum. **Head** (Figs. 61-62): pubescence white, rarely tinged faintly with pale yellow on vertex. (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with moderately small, scattered punctures below, becoming subcontiguous to contiguous above. (3) *Interocular area* rugose below, becoming rugulose to coarsely punctate above; supraclypeal area shallowly punctate to weakly rugose. (4) *Vertex* contiguously and coarsely punctate to rugulose anteriorly, becoming contiguously and less coarsely punctate laterally; area behind and between ocelli weakly rugulose. (5) *Gena* with numerous moderately fine, contiguous carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* amber; very short. (7) *Mandible* yellow with apical ⅓ ferruginous. (8) *Antenna* with scape sometimes black, but usually yellow with brown or black on apical ½ of upper surface; pedicel brown below, brown-black above; flagellum brown to brown-black above, pale amber to brown below. **Mesosoma:** pubescence white, rarely tinged faintly with very pale yellow on mesoscutum. (9) *Pronotum* as in ♂. (10) *Mesoscutum* with medium-sized, moderately deep, contiguous punctures, becoming finely rugose anteriorly and moderately rugose antero-laterally. (11) *Mesoscutellum* with punctures like those of mesoscutum but sometimes less dense and subcontiguous laterally. (12) *Metanotum* moderately finely and shallowly rugose. (13) *Mesepisternum* moderately coarsely and deeply rugose. (14) *Metepisternum* rugose (like mesepisternum) to horizontally carinate with carinae anastomosing most often near posterior margin. (15) *Propodeum* with strong propodeal carina; propodeal shield very faintly rugose; dorsal area moderately to coarsely rugose; lateral area with shallow, horizontal, anastomosing rugae, very fine to moderately fine anteriorly, becoming much coarser and slightly deeper posteriorly. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but with metallic green tints on proximal margin. (18) *Fore leg* with coxa brown to brown-black, tinged with metallic green; trochanter sometimes black, but usually pale amber with yellow on distal ½ of anterior surface; femur entirely yellow to brown-black with small yellow spot dorsally at apex; tibia yellow to brown with yellow antero-dorsally on basal ⅘; and tarsus yellow to brown. Pubescence white to amber. (19) *Middle leg* like fore leg but dark specimens with faint metallic tints on trochanter and with yellow area on tibia reduced to small spot dorsally at base; pubescence like that of fore leg but faintly fuliginous on darker specimens. (20) *Hind leg* with coxa bright metallic green dorsally and brown, strongly tinged with metallic green elsewhere; trochanter brown to brown-black; femur, tibia and tarsus pale amber to brown-black. Pubescence white to pale amber, becoming fuliginous basally on dorsal area of tibia of darker specimens.

Metasoma: (21) *Terga* pale amber with small black spots laterally on terga 3-4 to entirely black with distal margins transparent (see preceding discussion of variation). Pubescence white, becoming pale amber around pygidium; bands of dense tomentum on basal halves of terga 2-5, and centrally on tergum 1 (often interrupted medially on tergum 1); short, appressed, inconspicuous hairs distal to bands of tomentum; moderately long hairs anteriorly on tergum 1, ventro-laterally on terga 1-5, and dorsally on terga 5-6. (22) *Sterna* pale amber to black with scattered, long, white hairs on exposed areas.

Agapostemon mexicanus n. sp.

The name of this species refers to the country where it is found.

The male holotype and the three male paratypes are labeled, "14 mi. S./El Arco Mine/L. Cal. VI-23-38//Michelbacher & Ross Collectors." The allotype is labeled, "Mesquital/L. Cal. VII-28-38//Michelbacher & Ross Collectors." All of these types are in the California Academy of Sciences, San Francisco.

Distribution. In addition to the localities listed above I have seen specimens from: Santa Maria Valley (3 ♂, 11 Aug.), Magdalena Bay (1 ♂, 30 May), and 28 miles south of El Arco, Baja California, Mexico (1 ♀, 3 July); 25 miles south of Navajoa, Sonora, Mexico (1 ♀, 13 Sept.); 17 miles south of Navajoa, Sonora, Mexico (1 ♂, 18 Aug.).

Diagnosis. The male may be distinguished from all other North American species of *Agapostemon* by the comb of 14-20 large, evenly spaced submarginal bristles on metasomal sternum 4. The female may be distinguished from *A. splendens, A. texanus, A. angelicus, A. femoratus, A. cockerelli* and *A. aenigma* by its black metasoma; from *A. melliventris, A. peninsularis, A. nasutus, A. leunculus* and *A. intermedius* by the absence of yellow on its clypeus; from *A. erebus* and *A. atrocaeruleus* by the bright metallic green to blue-green of its head and mesosoma; and from *A. tyleri* by the lack of a smooth shiny area (with scattered punctures) centrally on its supraclypeal protuberance.

Description

male (Figs. 90-91, 156, 189, 204)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma banded with black and yellow. **Head** (Figs. 90-91): pubescence white, becoming yellowish on interocular area and vertex. (1) *Labrum* as in *A. texanus* but slightly more obtuse apically. (2) *Clypeus* as in *A. melliventris* but with medial enlargement of yellow band not quite as prominent. (3-7) *Interocular area, vertex, gena, malar area* and *mandible* as in *A. melliventris*. (8) *Antenna* brown-black with scape and pedicel

yellow below, flagellum pale amber below. **Mesosoma:** pubescence white, becoming yellowish on mesonotum and metanotum. (9-12) *Pronotum, mesoscutum, mesoscutellum* and *metanotum* as in *A. melliventris.* (13) *Mesepisternum* more coarsely rugose than metanotum (especially anteriorly). (14-15) *Metepisternum* and *propodeum* as in *A. melliventris* but with finer sculpturing. (16) *Wing* as in *A. melliventris* but veins darker brown. (17) *Tegula* as in *A. melliventris* but with metallic green tints basally and with transparent areas very pale amber. (18-20) *Fore, middle* and *hind legs* as in *A. peninsularis* but with brown-black streak on tibiae posterior (Fig. 156). **Metasoma:** (21) *Terga* as in *A. peninsularis* but with pubescence shorter and less dense. (22) *Sterna* 2-4 yellow with brown submarginal band posteriorly, sterna 5-6 brown, sternum 1 with metallic green tints basally; pubescence long and pale on brown areas; sternum 4 with low submarginal ridge posteriorly and row of 14-20 large, evenly spaced bristles just distal to submarginal ridge. (23) *Genitalia* (Figs. 189, 204) with medium-sized ventral lobe on gonocoxite fringed with hairs.

FEMALE (Figs. 63-64)

General coloration of head and mesosoma bright metallic green, metasoma black. **Head** (Figs. 63-64): as in *A. melliventris* but lower margin of clypeus black instead of yellow and with pubescence becoming slightly fuliginous at vertex. **Mesosoma:** pubescence white, becoming fuliginous on mesonotum and metanotum. (9-15) *Pronotum, mesoscutum, mesoscutellum, metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. melliventris* but with finer sculpturing. (16) *Wing* hyaline with veins brown, radius much darker than other veins. (17) *Tegula* as in *A. melliventris.* (18) *Fore leg* brown-black with faint metallic green on coxa and with yellow to pale amber anteriorly and dorsally on tibia and apically on femur. (19-20) *Middle* and *hind legs* brown to brown-black with hind coxa metallic green dorsally and tinged with metallic green anteriorly. Pubescence dark brown dorsally on tibiae. **Metasoma:** (21) *Terga* brown-black to black. Pubescence white becoming brown-black around pygidium; moderately long, becoming short and appressed dorsally; dense tomentum on basal third of terga 2-5, sparse tomentum on anterior ⅔ of tergum 1. (22) *Sterna* brown to brown-black with metallic green tints basally on sternum 1; pubescence white and moderately long.

Agapostemon mourei n. sp.

This species is named after Padré J. S. Moure who has contributed so much to knowledge of the South American bee fauna.

The male holotype, the allotype and the paratypes (16 ♂, 2 ♀) are all labeled, "Region Chapare/ Bolivia 400 M./ VIII 1950 Zischka." All of

these types are in the Snow Entomological Museum at the University of Kansas.

Distribution. This species seems to be sympatric with *A. boliviensis*. In the Snow Entomological Museum I have seen additional specimens (14 ♂, 3 ♀) from the type locality and specimens labeled as follows: "BOLIVIA-Beni, Rur-/ renabaque, 175 mts./ 5 October 1956/ (L. Pena)" (6 ♂); same as preceding but collected Oct. 17 (3 ♂); "BOLIVIA-Beni, Rey-/es. 10 December/ 1956 (L. Peña)" (2 ♂); "BOLIVIA- Chapare,/ Tropical Reg. 400/ mts. August 1951 (Zischka)" (3 ♂); same as preceding but 25 August 1950 (1 ♂); same as preceding but Oct. 1953 (5 ♂); "Cristal Mayu./ Chapare, Cochabamba Bol. 200 m./ VIII-4-49 L E Pena" (1 ♂); "Prov. del Sara/ Bolivia, 450 m./ J. Steinbech// Acc. 4548" (1 ♂); same as preceding but Acc. 5072 (1 ♂). In the U.S. National Museum I have seen specimens labeled: "nr. mouth/ Rio Mapiri/ Sept// Mulford/ BioExpl/ 1921-22" (3 ♂); "Covendo/ Boliv./ W M Mann// September// Mulford/ BioExpl/ 1921-22" (1 ♀); "Ixiamas/ Bolivia/ W M Mann// Dec// Mulford/ BioExpl/ 1921-22" (2 ♂); "Rosario, Lake/ Rogagua, Boliv/ W M Mann, Oct / 28-Nov. 9, 1921// Mulford/ Biol. Expl.,/ 1921-1922" (2 ♂).

Diagnosis. The male may be distinguished from most other species by the presence of a medial "button" at the base of its last visible (6th) sternum. This sternal "button" is narrowed basally unlike that of the closely related *A. inca* (Figs. 139-140), and the hind femur, tibia and basitarsus are less slender than those of *A. inca* (Figs. 167-168). *Agapostemon mourei* may be distinguished from the related *A. lanosus, A. boliviensis* and *A. intermedius* by the larger and differently shaped medial plate of its gonostylus (Figs. 176, 177A-B, 192).

The female may be distinguished from most other species by the acute lateral angle and posterior lobe of its pronotum (Figs. 132-133) and by the dense woolly pubescence of its mesoscutum. It may be distinguished from *A. lanosus* by its bright yellow clypeal band and shallower genal striae; from *A. boliviensis* by its finer sculpturing and paler pubescence; from *A. heterurus* by the yellow on its clypeus and by the coppery luster of its head and mesosoma.

Variation. The general appearance of the males varies strikingly because the black markings of the appendages and metasoma are frequently replaced by pale amber markings.

Description

male (Figs. 127-128, 132-133, 139, 167, 176, 217)

General coloration of head and mesosoma bright metallic green to blue, metasoma with black and yellow or amber and yellow bands. **Head** (Figs. 127-128): with short creamy to yellow pubescence on interocular area and

vertex, becoming long and creamy to white on gena. (1) *Labrum* opaque lemon yellow with transparent pale amber margins, ¾ as long as wide; antero-lateral margins forming obtuse angle at apex; large transverse ridge on basal ⅓ without median depression. Punctures on crown of basal ridge shallow and separated by several times their diameters; submarginal punctures large and shallow at apex becoming smaller laterally and disappearing just anterior to lateral margins of basal ridge. Pubescence restricted to minute scattered hairs on crown of basal ridge and single submarginal row of simple hairs deflected distally from antero-lateral margins. (2) *Clypeus* with large, shallow, sparsely scattered shallow punctures on lower (yellow) ½-⅔, becoming more abundant, slightly smaller and contiguous on upper (green) ⅓-½. (3) *Interocular area* with small, deep, contiguous punctures below ocelli, becoming medium-sized at level of antennal sockets and shallower, subcontiguous and smaller below antennae; supraclypeal protuberance with medium contiguous moderately deep punctures. (4) *Vertex* with small, deep, contiguous punctures anteriorly and laterally, becoming shallower and slightly larger between ocelli; transversely carinate posteriorly. (5) *Gena* with parallel, subcontiguous, short, weak carinae extending dorsolaterally from antero-ventral margin. (6) *Malar area* yellow, short, and with minute hairs. (7) *Mandible* yellow with apical ¼-⅓ amber. (8) *Antenna* dark brown to black, scape and pedicel yellow below. **Mesosoma:** pubescence short, pale fulvus to yellow on mesoscutum and mesoscutellum, becoming shorter and creamy to white posteriorly and ventrolaterally. (9) *Pronotum* (Figs. 132-133) with lateral angle and posterior lobe acutely pointed, lateral angle enlarged and projecting antero-laterally; with conspicuous sharp carina extending postero-ventrally from apex of lateral angle; with weak irregular rugae postero-laterally. Pubescence above lateral angle and posterior lobe pale fulvus to yellow, creamy to white below. (10) *Mesoscutum* with very large, conspicuous flange laterally on anterior margin extending antero-dorsally; punctures very fine, deep and contiguous. (11) *Mesoscutellum* with punctures slightly larger and shallower than those of mesoscutum and subcontiguous. (12) *Metanotum* deeply and moderately coarsely rugose. (13) *Mesepisternum* coarsely rugose anteriorly, becoming moderately rugose posteriorly. (14) *Metepisternum* moderately rugose with horizontal rugae slightly more prominent than other rugae. (15) *Propodeum* with propodeal carina nearly obliterated by extremely coarse and deep rugae posteriorly and dorsally; posterior and dorsal rugae becoming moderately fine, deep, contiguous punctures antero-laterally. (16) *Wing* sub-hyaline, tinted with amber on distal margins, veins and stigma brown. (17) *Tegula* pale transparent amber with anterior, submarginal, yellow crescent. (18) *Fore leg* yellow with brown streak posteriorly on coxa, trochanter, femur and tibia. (19) *Middle leg* elongate, yellow with brown

markings on posterior of trochanter, tibia and sometimes femur. (20) *Hind leg* (Fig. 167): femur sub-globose, tibia and basitarsus inflated. Coxa yellow below, dark brown with strong metallic tints above, trochanter dark brown, femur dark brown with yellow antero-dorsally, tibia dark brown sometimes streaked with yellow dorsally, and basitarsus varying from dirty yellow to dark brown. **Metasoma:** (21) *Terga* 2-6 very pale amber to dark brown-black on posterior ⅔ and yellow on anterior ⅓ (often partially concealed by overlap), tergum 1 with amber to brown-black band on anterior margin and brown to amber on anterior face; large, conspicuous, subcontiguous punctures anteriorly on tergum 1 becoming smaller posteriorly on tergum 1 and progressively smaller on posterior terga. Pubescence sparse and yellowish. (22) *Sterna* dark brown and with yellow or amber markings on sterna 1-3; sternum 6 (Fig. 139) with proximo-medial projection, or "button," with each lateral flange slightly more than ½ width of base (as measured on transverse section through widest part of "button"); pubescence moderately long, scattered, and pale fulvus to yellowish on exposed areas. (23) *Genitalia* (Figs. 176, 217).

female (Figs. 125-126)

General coloration dark copper with tints of metallic green. **Head** (Figs. 125-126): with pubescence fulvus, becoming creamy on genal region. (1) *Labrum* dark amber to ferruginous. Basal ridge prominent, proximal face sloping gently toward proximal margin, distal face sharply declivous and delimited from basal area by carina; additional carina present between basal area and distal process; distal region narrow, rounded apically and with large central keel. Pubescence restricted to single submarginal row of coarse, stiff, amber bristles curving anteriorly at their apices and forming fimbria on antero-lateral margins of labrum. (2) *Clypeus* with shallow medial concavity; submarginal, yellow band broadly interrupted medially; punctures widely scattered on lower ½, becoming sub-contiguous on upper ½. (3) *Interocular area* with fine, moderately deep, contiguous punctures below ocelli, becoming finely rugose laterally and below; supraclypeal protuberance with moderate-size, subcontiguous punctures. (4) *Vertex* with fine, moderately deep, contiguous punctures anteriorly and laterally, and with fine, transverse striae posteriorly. (5) *Gena* with regular fine carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* amber to brown-black, very short, pubescence minute, white, appressed hairs. (7) *Mandible* yellow with apical ⅓ ferruginous. (8) *Antenna* dark brown to brown-black with flagellum pale yellowish amber below. **Mesosoma:** pubescence short, dense, woolly and pale ferruginous on meso- and metanotum, becoming sparse, moderately long and slightly paler below. (9) *Pronotum* like that of ♂ (Figs. 132-133) but with dense fulvus hair above lateral angle and posterior lobe. (10) *Mesoscutum* with small, deep,

contiguous punctures. (11) *Mesoscutellum* with punctures slightly smaller and shallower than those of mesoscutum. (12) *Metanotum* finely punctorugulose. (13) *Mesepisternum* with moderately coarse, shallow rugae anteriorly, becoming slightly finer posteriorly. (14) *Metepisternum* shallowly rugose with horizontal rugae predominant. (15) *Propodeum* with prominent propodeal carina; propodeal shield coarsely rugose, with horizontal rugae predominant; dorsal area coarsely and deeply rugose; lateral area with moderately coarse, deep striae extending from propodeal carina to anterior margin. (16) *Wing* as in ♂. (17) *Tegula* as in male, but slightly darker amber. (18) *Fore leg* brown with amber anteriorly on femur and tibia as well as dorsally and posteriorly; pubescence amber, becoming brown dorsally on tibia and tarsus. (19) *Middle leg* brown with amber anteriorly on tibia and femur and posteriorly on femur; pubescence pale amber, becoming dark brown to brown-black dorsally on tibia and tarsus. (20) *Hind leg* brown to brown-black, pubescence pale amber, becoming dark brown to black antero-dorsally on tibia and basitarsus. **Metasoma:** (21) *Terga* finely and contiguously punctate anteriorly with punctures becoming smaller and shallower posteriorly; amber with yellow on basal ⅓ of terga 2-5 and brown apically on tergum 5; pubescence short and sparse, pale amber anteriorly and dark brown posteriorly. (22) *Sterna* pale amber with brown basally on sterna 1, 4-6; long, sparse, yellowish pubescence on exposed areas.

Agapostemon nasutus Smith

Agapostemon nasutus Smith 1853. Type ♂, British Museum (Natural History).
Agapostemon peruvianus Cameron 1903 **(new synonymy).** Type ♂, British Museum (Natural History).
Agapostemon nasutus gualanicus Cockerell 1912a **(new synonymy).** Type ♂, U.S. National Museum.
Agapostemon purpureopictus Cockerell 1924 **(new synonymy).** Type ♀, California Academy of Sciences, San Francisco.
Agapostemon melanurus Cockerell 1949 **(new synonymy).** Type ♀, U.S. National Museum.

I have seen the types of all the above forms except *A. nasutus* and *A. peruvianus,* which were examined for me by Michener. There is no doubt that they are all the same species. *A. nasutus gualanicus* Cockerell is an ill-defined geographic variant which does not seem to warrant formal recognition as a subspecies (see discussion of variation).

DISTRIBUTION (Fig. 7). *Agapostemon nasutus* is the most common and widespread of the tropical *Agapostemon.* Absent from the central plateau of Mexico, it occurs along the eastern coast as far north as Brownsville, Texas, and along the western coast as far north as Hermosillo, Sonora, and El Arco, Baja California. It is widespread in southern Mexico and Central America but has not been found in the wet Atlantic lowlands of Nicaragua, Costa Rica and Panamá. It has been collected along the coast of Venezuela as

far east as Trinidad, in the Cauca and Magdalena valleys of Colombia, and west of the Andes as far south as Ica, Perú.

It has been collected at or near sea level throughout its range and at elevations as high as 8,500 ft. (2,591 m) at Calderon, Ecuador; 1,200 m (3,963 ft.) at San José, Costa Rica; 5,000 ft. (1,524 m) at Guatemala City, Guatemala; and 6,400 ft. (1,951 m) at Tecamachalco, Puebla, Mexico. It has been collected in South America in every month but October, in Central America in every month but December and in Mexico north of the Isthmus of Tehuantepec in every month but January. Thus it seems that this species flies most, if not all, of the year wherever it occurs. My field observations in Costa Rica indicate that it is hard to find toward the end of the dry season, when flowers are also scarce.

Diagnosis. Males are easily distinguished from all other species by the unique "hog-nosed" appearance of the broad, concave, ventral portion of the short clypeus (Figs. 85-87) and by sternum 6 which is broad with laterally directed disto-lateral tufts of branched hairs usually visible from above. Females, as well as males, may be distinguished from all other species without acutely pointed lateral pronotal angles by a yellow or creamy spot at the apex of the rounded posterior lobe of the pronotum (Fig. 134).

Variation. The females normally are metallic green on the head and thorax but in the central highlands of Central America (e.g., Gualán, Guatemala and San José, Costa Rica) the green is replaced by blue. This is the form named *A. nasutus gualanicus* by Cockerell. The same blue color is also found in many females from the southern limits of the range (e.g., Lima, Perú) and the northern limits of the range (e.g., Brownsville, Texas and Hermosillo, Sonora) where it may be very dark purple-blue.

Normally black, the abdomen is pale amber in the majority of females from coastal Venezuela. I have seen females with black or intermediate abdomens from this same region although these constitute less than 10% of the total sample (Fig. 7).

The amount of yellow on the males and females is quite variable and is slightly correlated with the coloration of the head and mesosoma of females. Blue females fly with males usually more extensively marked with black or brown than are males from regions where the metallic color of the females is green.

Description

male (Figs. 85-87, 153, 195, 221-223)

General coloration of head and mesosoma metallic green to blue-green or bronze, metasoma yellow with black bands. **Head** (Figs. 85-87): (1) *Labrum* yellow, 40% as long as broad, flattened basal area slightly concave, 20% as long as broad, distal area triangular, 85% as long as basal width and separated from it by sharp step. Distal area shiny, impunctate; basal area

with scattered punctures most abundant distally. Distal margin with row of about 32 widely separated bristles, stout medially, finer laterally, remainder of distal area glabrous; basal area with scattered, prostrate hairs directed distally, longest and most abundant distally and forming fringe on distal margin of basal area. (2) *Clypeus* with ventral area smooth and shiny, dorsal area shiny and coarsely punctate; flattened ventral area glabrous, at right angle to upper area which is densely covered with white to yellowish hairs. (3) *Interocular area* with dense, fine punctures below vertex, rugose laterally, coarsely punctate or rugose above antennal sockets; pubescence dense, white to yellowish hairs nearly as long as scape and much shorter along inner margins of eyes. (4) *Vertex* with dense fine punctures below and in ocellar triangle; coarsely and shallowly rugose behind ocellar triangle. (5) *Gena* with sparse, weak carinulae extending postero-dorsally from antero-ventral margin; pubescence dense, white (never yellowish), medially about 1.5 times as long as on interocular area. (6) *Malar area* yellow; pubescence sparse, white, tomentose. (7) *Mandible* yellow with apical third transparent ferruginous; nearly straight, not strongly curved as in other species. Pubescence on flat outer surface and posterior margin white to yellowish and directed apically; single longitudinal row of short simple bristles on inner surface. (8) *Antenna* (except scape and last two flagellomeres) dark brown above and light brown to yellow below; scape yellow with brown on apical ¼-½ above; last flagellomere brown with pale spot on upper side at apex; penultimate flagellomere brown, becoming yellow or light brown on basal ½ of underside. **Mesosoma:** metallic green, blue-green or bronze, with yellow or creamy spot on apex of posterior lobe of pronotum; moderately dense, white or creamy pubescence evenly distributed on all but anterior and lateral surfaces of pronotum. (9) *Pronotum* with lateral angle and posterior lobe rounded; 2-4 inconspicuous parallel carinae slanting rearwards and downwards near postero-lateral margin. Tomentum on lower lateral area white. (10) *Mesoscutum* densely covered with moderately deep, confluent punctures, fine posteriorly, becoming shallowly rugose on anterior ¼-⅓. (11) *Mesoscutellum* with fine, moderately deep punctures separated by about their own diameters. (12) *Metanotum* moderately and shallowly rugose medially, rugulose laterally. (13) *Mesepisternum* coarsely and shallowly rugose anteriorly, becoming moderately rugose posteriorly. (14) *Metepisternum* with weak, parallel, interconnected, horizontal carinulae. (15) *Propodeum* coarsely and shallowly rugose laterally, rugae slightly coarser and deeper dorso-medially; propodeal carina weak, evenly rounded dorsally; propodeal shield weakly and irregularly carinulate. (16) *Wing* pale, transparent brown, not darkened apically, radius much darker than other veins. (17) *Tegula* yellow with large transparent area in center of posterior half and transparent on posterior, distal and anterior margins.

(18) *Fore leg* yellow, sometimes with brown on posterior surface of coxa, trochanter and base of femur. Pubescence on coxa, trochanter and basal ½ of femur sparse, long, white and branched; on tarsus, tibia and apex of femur sparse, short, simple, white to yellowish. (19) *Middle leg* yellow, coxa brown; trochanter and posterior area of femur sometimes brown; pubescence like that of fore leg. (20) *Hind leg* (Fig. 153) with coxa brown, becoming green dorsally; trochanter brown; brown streak on basal ¾ of posterior surface of femur; tibia and tarsus yellow; on some specimens with brown on basal ¾ of tibia and all but anterior of femur; pubescence similar to that of preceding legs except posterior surfaces of basitarsus and femur which are densely covered with short, stiff, simple, yellow hairs directed distally. **Metasoma:** (21) *Terga* 1-6 transparent apically, each with subapical brown or black band slightly broader than transparent area (may seem broader if abdomen is flexed and brown basal band of underlying tergum shows through overlapping transparent margin of preceding tergum), central yellow band almost twice as wide as subapical black band, and narrow brown or black basal band; tergum 1 with additional yellow basal region; tergum 7 brown or black; pygidial plate fawn to yellow. Pubescence fine and short dorsally, longer laterally, at base of tergum 1, and on posterior margins of terga 5-7; white except on dark portions of terga 5-7 where yellow or brown; terga shiny with small, shallow punctures separated by about their own diameters. (22) *Sterna* 2-5 yellow, each with subapical brown band, apical margin transparent, narrow brown basal band often concealed by overlap of preceding sternum but sometimes so broad as to be confluent with subapical brown band; sternum 1 brown, tinged with green basally, paler subapically, distal and lateral margins transparent; sternum 6 yellow with basal brown band and transparent distal margin; yellow areas on abdominal sterna sometimes partially or completely replaced by brown; sternum 6 very broad with disto-lateral bulge and longitudinal medial ridge; sternum 1 with few scattered long white hairs and thin fringe of short hairs on distal margin; sterna 2-5 with scattered long yellow hairs subapically, distal margins fringed with short, prostrate hairs, basal ¼ of each with minute, simple, white hairs; sternum 6 with numerous long yellowish hairs conspicuously branched, short medially but with long disto-lateral tufts directed postero-laterally and usually visible from above. (23) *Genitalia* (Figs. 195, 221-223) far more complex than those of other species, and relatively large.

FEMALE (Figs. 41-42, 134)

General coloration of head and thorax metallic green to blue. Metasoma black or pale amber, with white bands of fine pubescence. **Head** (Figs. 41-42): pubescence short (½-¼ as long as shortest distance between antennal sockets) and white or yellowish on face, twice as long on gena and pure

white. (1) *Labrum* dark amber to ferruginous. Basal ridge prominent, proximal face sloping gently toward proximal margin, distal face sharply declivous, and apex of ridge with deep punctures; distal portion narrow, abruptly rounded at apex; conspicuous median keel on antero-distal portion, continued basally almost to basal ridge; anterior margin of keel flattened and slightly flared laterally; single row of dark amber, wide, flat, stiff bristles curving anteriorly at their apices forming fimbria on lateral margins of distal portion of labrum. (2) *Clypeus* green above with yellow band on lower ½-⅔ bordered with black; yellow almost entirely replaced with dark brown or black on darker specimens; median subapical area slightly concave, yellow band with large scattered punctures, upper green area with numerous short horizontal carinulae or horizontally elongate punctures. (3) *Interocular area* coarsely and shallowly rugose, supraclypeal protuberance with dense, long, horizontal carinulae. (4) *Vertex* densely and finely punctate between, anterior to, and lateral to ocelli; coarsely and shallowly rugose behind ocelli. (5) *Gena* with numerous weak, contiguous rugulae running postero-dorsally from antero-ventral margin. (6) *Malar area* brown and very short. (7) *Mandible* yellow, apical ⅓ ferruginous. (8) *Antenna* dark brown to black, slightly paler brown on underside of flagellum. **Mesosoma:** pubescence (except on pronotum) nearly twice as long as on face, moderately dense, white laterally and below, but may be yellowish or fuliginous on mesoscutum and mesoscutellum of blue specimens. (9) *Pronotum* (Fig. 134) with yellow to creamy spot at apex of posterior lobe; lateral angle and posterior lobe rounded as in ♂; faint punctures on dorsal portion and faint parallel striae running downward and rearward on lower lateral area; pubescence white, very fine, short, and appressed on lower lateral area. (10) *Mesoscutum* as in ♂. (11) *Mesoscutellum* finely and densely punctate anteriorly, becoming coarsely punctate posteriorly; shiny, less densely punctate area lateral to center. (12) *Metanotum* rugulose. (13) *Mesepisternum* coarsely rugose anteriorly, somewhat less coarsely so posteriorly. (14) *Metepisternum* as in ♂. (15) *Propodeum* coarsely rugose dorsally and postero-laterally, becoming finely striate antero-ventrally; propodeal carina prominent, strongly curved dorso-laterally, weakly convex dorsally; propodeal shield with irregularly anastomosing carinulae running laterally and slightly upward from mid-line. (16-17) *Wing* and *tegula* as in ♂. (18) *Fore leg* brown to black with yellow on anterior apical ⅓ of femur and basal ⅔ of tibia, may be more extensive on pale specimens; pubescence of coxa, trochanter and femur white, becoming yellow on tibia and tarsus. (19) *Middle leg* similar in color and pubescence to fore leg but pubescence on dorsal surface of tibia and tarsus fuliginous. (20) *Hind leg* brown to black, pubescence similar to that of middle leg but even darker on dorsal surface of tibia and tarsus and with pale penicillus at apex of

basitarsus. **Metasoma:** (21) *Terga* usually black but often pale amber with black at apices of terga 4-6 in Colombian and Venezuelan specimens; anterior vertical portion of tergum 1 with sparse white hairs, upper ½ with thin white tomentum; basal halves of terga 2-4 with dense white tomentum; prepygidial fimbria and hairs adjacent to pygidium and on apical portion of tergum 4 brown to black. (22) *Sterna* brown to black, often pale amber in Colombian and Venezuelan specimens; long, scattered, whitish pubescence on exposed portions.

Agapostemon obscuratus Cresson

Agapostemon obscurata Cresson 1869. Type ♂ (not ♀), Academy of Natural Sciences, Philadelphia.

Agapostemon obscuratus. Dalla Torre, 1896.

Agapostemon obscuratus abjectus Cockerell 1917b **(new synonymy)**. Type ♂ (not ♀), U.S. National Museum.

By peculiar coincidence the descriptions by both Cresson and Cockerell are headed by the symbol "♀", but both descriptions are of males. I have seen the types of *A. obscuratus* and *A. obscuratus abjectus* and both specimens are males. The color differences described by Cockerell were not visible to me.

The specific rank of *A. obscuratus* is questionable, as I am unable to find any differences between specimens of *A. viridulus* and *A. obscuratus* other than the replacement of metallic coloration on the former by dark green-black on the latter. The sympatric distribution of *A. obscuratus* and *A. viridulus* and the absence of intermediate forms seems to refute any contention that they are merely subspecies. It is possible that they are a single species with two color phases. In the absence of biological data, I choose the simplest solution and regard *A. obscuratus* as specifically distinct from *A. viridulus*.

Distribution. I have seen specimens from Habana, Cuba (Jan., 4 ♂; Feb., 2 ♂; April, 1 ♂; Sept., 1 ♂; Dec., 3 ♂; 15 ♂ and 2 ♀, no date).

Diagnosis. Both sexes may be distinguished from all other West Indian species of *Agapostemon* by their total lack of metallic coloration.

Description. As in *A. viridulus* but for the color differences mentioned above.

Agapostemon ochromops n. sp.

The name of this species refers to the pale yellowish eyes of both sexes.

The male holotype is labeled, "Bahamas/Mariguana [Mayaguana?] /22-II//Greenway/coll." The female allotype and paratype are labeled, "Bahamas/Mariguana [Mayaguana?] /25-II / fls. *Cakile* / Fairchild coll." All of these types are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Distribution. Aside from the type series listed above, I have seen

specimens collected on the following Bahamian islands: Rum Cay (Feb.; 23 ♂, 3 ♀), Cat I. (March; 1 ♀), Concepsion [Conception?] I. (Feb.; 9 ♂, 1 ♀) and New Providence I. (1 ♂).

DIAGNOSIS. Both sexes may be distinguished from *A. centratus, A. kohliellus, A. obscuratus, A. hispaniolicus, A. viridulus, A. swainsonae, A. cubensis, A. alayoi, A. insularis, A. jamaicensis, A. poeyi, A. viequesensis, A. columbi* and *A. aenigma* by their pale milky eyes and creamy to yellow pigment on the underside of the pterostigma. The female is metallic green in contrast to the metallic dark blue of *A. sapphirinus* and the metallic dark purple of *A. cyaneus*. The male may be distinguished from *A. cyaneus* by the pale yellow to amber of the underside of its pedicel but is indistinguishable from males of *A. sapphirinus*.

VARIATION. The anterior surface of the first metasomal tergum of the allotype is honey-colored with an interrupted yellow band. On the other males the honey-color is replaced by light to dark brown. The brown on the legs is lightest on the allotype and darker on the other males. Metallic color varies in intensity and varies from blue-green to green both between and within island populations. The genal carinulae of females are finest and most numerous on the specimen from Conception I., most coarse and fewest on specimens from Rum Cay, and intermediate on the holotype and paratype from Mariguana (Mayaguana?) I.

This is the most heterogeneous of the Bahamian species and it may be a composite species. Only more collections from the Bahamas can resolve the problem.

DESCRIPTION

MALE (Fig. 225)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma brown to amber banded with yellow. **Head:** as in *A. viequesensis* but with eyes pale milky to yellowish, and ferruginous apical portion of mandible slightly reduced. **Mesosoma:** as in *A. viequesensis* but with slightly coarser sculpturing, with creamy to yellow pigment on pterostigma and on underside of larger wing veins. **Metasoma:** as in *A. viequesensis* but pygidium with apex more acute (Figs. 224-225), metasomal terga 3-5 of the holotype and a specimen from Rum Cay with faint metallic tints and with pale bands slightly paler and dark bands slightly darker than in *A. viequesensis*, and genitalia with apex of distal stylus of gonostylus more spoon-shaped than in *A. viequesensis* (but not so much as in *A. poeyi*).

FEMALE

Like *A. viequesensis* but with eyes milky to yellowish; with creamy to yellow pigment on pterostigma and underside of larger wing veins; and with

sculpturing less coarse than in *A. poeyi,* but coarser than in *A. viequesensis* (closer to the latter), and somewhat more variable than in other West Indian species (even within island populations).

Agapostemon peninsularis n. sp.

The name of this species refers to the Baja California peninsula where it is found.

The male holotype, the allotype and nine male paratypes are all labeled, "Mgdlena Bay/Lower Cal./May 30, 1925//H. H. Keifer/Collector" and are all in the California Academy of Sciences, San Francisco.

Distribution. In addition to the type locality above I have seen specimens from the following localities: Ensenada (1 ♀, 31 May; 1 ♂, 24 June; 3 ♂, 30 Aug.), Camalu (1 ♀, 23 June), 3 miles south of San Quintin (3 ♀, 8-12 March), 20 miles west of San Augustine (1 ♂, 24 Sept.), and 20 miles north of Mesquital (1 ♂ & 1 ♀, 27 Sept.), Baja California, Mexico; San Diego (1 ♂) and La Jolla (1 ♂, 16 July), California.

Diagnosis. The male may be distinguished from most species by its lack of a prominent hind femoral tooth and by the black streak extending from the base of the posterior surface of its hind femur to the apex of the posterior surface of its hind tibia; and from *A. mexicanus* by the lack of enlarged submarginal bristles medially on its 4th metasomal sternum (only two to four submarginal bristles are present on each side). The female may be distinguished from many species by its black metasoma, bright green head and thorax, transverse yellow clypeal band, and rounded lateral pronotal angle; from *A. tyleri* by the lack of a smooth shiny (with scattered punctures) area centrally on its supraclypeal protuberance; from *A. nasutus* by the absence of a creamy spot on the apex of its pronotal lobe; from *A. leunculus* by the white to creamy pubescence (brown to black in *A. leunculus*) around the basitibial plate on its hind leg; from *A. melliventris* by the finely rugulose dorso-medial region of its propodeum (rugose in *A. melliventris*).

Description

male (Figs. 88-89, 157, 190, 205)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma banded with black and yellow. **Head** (Figs. 88-89): pubescence white. (1) *Labrum* as in *A. texanus* but more obtuse apically. (2) *Clypeus* as in *A. melliventris* but with transverse yellow band slightly narrower and with medial enlargement only about ½ as great. (3-5) *Interocular area, vertex* and *gena* as in *A. melliventris* but with sculpturing slightly coarser. (6-7) *Malar area* and mandible as in *A. melliventris.* (8)

Antenna with scape and pedicel brown-black above and yellow below to entirely brown-black; flagellum brown-black above, becoming pale amber to yellow below. **Mesosoma:** pubescence white. (9-12) *Pronotum, mesoscutum, mesoscutellum* and *metanotum* as in *A. melliventris*. (13) *Mesepisternum* more coarsely rugose than metanotum (especially anteriorly). (14) *Metepisternum* with interconnected horizontal carinulae, becoming rugose posteriorly in some specimens. (15) *Propodeum* with propodeal carina usually absent but may be visible as very weak carina dorsally; propodeal shield very coarsely and shallowly rugose; dorsal area moderately rugose laterally, becoming very finely and shallowly rugose medially; lateral area coarsely and shallowly rugose posteriorly, becoming moderately finely rugose anteriorly. (16) *Wing* as in *A. melliventris* but with veins darker brown. (17) *Tegula* pale transparent amber with submarginal yellow band anteriorly and posteriorly, and with strong metallic tints basally. (18) *Fore leg* with coxa metallic green; trochanter brown-black with metallic green tints basally and apical yellow spot anteriorly; femur yellow with broad brown-black streak postero-dorsally extending from base almost to apex; tibia yellow with brown-black streak ventrally; tarsus yellow. (19) *Middle leg* as fore leg but with brown-black ventral streak on tibia extending to posterior surface. (20) *Hind leg* (Fig. 157) as fore leg but with yellow spot on trochanter ventral; with brown to brown-black streak on femur posterior, extending to apex, and extending dorsally at apex; tibia with brown to brown-black streak posterior and extending dorsally at base and apex. Femur without distinct tooth and basitarsus without apical groove or basal ridge. **Metasoma:** (21) *Terga* 2-6 black with yellow band on basal ½ (usually partially obscured by overlapping terga posteriorly); tergum 1 black with yellow band centrally; terga 1-6 with posterior and ventro-lateral margins transparent; tergum 7 with pygidium dark amber to brown-black. Pubescence white, dark brown on postero-dorsal ½ of terga 1-4; moderately long, becoming short and appressed dorsally on terga 1-4. (22) *Sterna* 2-5 yellow with brown-black bands basally and anteriorly (these bands very narrow on sternum 2, becoming progressively broader on posterior sterna until yellow nearly absent on sternum 5), sternum 1 with strong metallic tints, sternum 6 brown-black with small medial ridge in shallow depression on apical ½. Pubescence long and pale on exposed areas, sternum 4 with 2-4 large hooked bristles at each postero-lateral margin. (23) *Genitalia* (Figs. 190, 205) with medium-sized ventral lobe on gonocoxite fringed with hairs.

FEMALE (Figs. 65-66)

General coloration of head and mesosoma bright metallic green, metasoma black. **Head** (Figs. 65-66): as in *A. melliventris* but with transverse band on clypeus narrower and bordered with brown-black, and with scape

entirely brown-black. **Mesosoma:** pubescence white, becoming creamy on mesonotum and pronotum. (9-14) *Pronotum, mesoscutum, mesoscutellum, metanotum, mesepisternum* and *metepisternum* as in *A. melliventris.* (15) *Propodeum* with weak propodeal carina; propodeal shield with large but very shallow rugae; dorsal area finely rugose laterally, becoming very finely rugulose medially; lateral area with shallow, anastomosing horizontal carinulae anteriorly, becoming shallowly rugose posteriorly. (16) *Wing* as in ♂. (17) *Tegula* as in *A. melliventris.* (18-19) *Fore* and *middle legs* with coxa dark brown tinged with metallic green; trochanter dark brown; femur dark brown with yellow apically; tibia yellow with dark brown streak ventrally; tarsus yellow. (20) *Hind leg* brown, coxa metallic green dorsally. **Metasoma:** pubescence white. (21) *Terga* brown-black to black. Pubescence moderately long, becoming short and appressed dorsally on terga 1-4; dense tomentum on basal ½ of terga 2-5 and on all but posterior ⅓ of tergum 1. (22) *Sterna* brown-black to black; moderately long pubescence on exposed areas.

Agapostemon poeyi (Lucas)

Andrena poeyi Lucas 1856. Type ♀, Gribodo collection, Museo Civico di Storia Naturale, Genoa.

Agapostemon festivus Cresson 1865 **(new synonymy).** Type ♂, Academy of Natural Sciences, Philadelphia.

Halictus (Agapostemon) chalcis Vachal 1903 **(new synonymy).** Type ♀, Naturhistorisches Museum, Vienna.

The "type" of *Andrena poeyi* has been examined by C. D. Michener. He states that it is labeled *"Andrena poeyi* Guérin *Cuba* Type" but notes that the word "type" is not in Guérin's hand. While this specimen may not be the type, I am regarding it as such until such time as a more likely candidate is found. The description coupled with the type locality leave little doubt as to the identity of this species. I have seen the type of *A. festivus* and it is obviously the male of *A. poeyi.* I have seen the type of *H. chalcis* and it is unquestionably conspecific with *A. poeyi.*

Distribution. I have seen about 70 specimens from Cuba; males have been collected in all months but January, June, October and December and females have been collected in January, April, June, September and November. I have also seen specimens from Guaiameti, Santo Domingo, Hispaniola (1 ♂, July); Arthurs Town, Cat I., Bahamas (1 ♀, July-Aug.); Mangrove Cay [part of Andros I.], Bahamas (1 ♀, 1 Aug.); Nassau, New Providence I., Bahamas (5 ♀, 12 Aug.; 1 ♀, Nov.; 1 ♂, 16 Dec.; 7 ♂ & 3 ♀).

I have also seen three males of this species labeled "Mexico-Veracruz, Nogales/April 1956/(N. L. H. Krauss)." In his revision of the banded subgenera of *Nomia,* D. W. Ribble (1965) noted specimens of the Cuban *Nomia robinsoni* with these label data and questioned the correctness of the labels.

In the face of this additional evidence it seems almost certain that the labels are incorrect.

DIAGNOSIS. Both sexes may be distinguished from those of *A. cyaneus, A. sapphirinus* and *A. ochromops* by their lack of milky to yellowish eyes or pterostigma. The male may be distinguished from *A. columbi* and *A. viequesensis* by its strong metallic green to blue tints medially on metasomal tergum 3; from *A. insularis* by its metallic blue to green tints postero-laterally on tergum 1; and from *A. jamaicensis* by its narrower hind femora. The female may be distinguished from *A. centratus, A. alayoi, A. obscuratus, A. hispaniolicus, A. viridulus* and *A. swainsonae* by its bright metallic green metasomal terga; from *A. viequesensis* by the basal green spot on its mandible; from *A. columbi* and *A. aenigma* by its conspicuous metallic green tints medially on metasomal sterna 3-4; from *A. insularis* by its rugose area adjacent to the parapsidal line.

DESCRIPTION

MALE (Figs. 144, 186, 210)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma dark brown with yellow bands. **Head:** color and shape as in *A. viequesensis;* sculpturing very slightly coarser than in *A. viequesensis;* pubescence of clypeus, interocular area and vertex yellowish to pale amber, that of gena white. **Mesosoma:** pubescence as in *A. viequesensis.* (9) *Pronotum* with lateral angle and posterior lobe more angular than in *A. viequesensis;* carinulae on postero-lateral area larger and fewer in number than in *A. viequesensis.* (10-12) *Mesoscutum, mesoscutellum* and *metanotum* as in *A. viequesensis* but with very slightly coarser sculpturing. (13-15) *Mesepisternum, metepisternum* and *propodeum* as in *A. viequesensis* but with much coarser sculpturing. (16) *Wing* as in *A. viequesensis* but with veins darker. (17) *Tegula* with dark amber to brown almost obscuring yellow band, metallic green tints antero-basally slightly more extensive than in *A. viequesensis.* (18-19) *Fore* and *middle legs* with coxae metallic green (only weakly tinted on middle leg), trochanters brown with amber to yellow on anterior surface, femora yellow with apical, brown postero-dorsal spot, tibiae yellow with brown postero-dorsally, and tarsi yellow to pale amber (some specimens from New Providence I. with brown areas on fore leg reduced); pubescence slightly darker than that of *A. viequesensis.* (20) *Hind leg* (Fig. 144) as in *A. viequesensis* but with brown areas much darker, with femur, tibia and basitarsus less swollen, and with ridge and apical groove on basitarsus narrower and less prominent. **Metasoma:** (21) *Terga* as in *A. viequesensis* but with brown areas darker, with apex of pygidium nearly as acute as that of *A. ochromops* (Figs. 224-225), and with metallic green replacing brown completely on terga 4-6 and partially on 2-3.

(22) *Sterna* as in *A. viequesensis* but slightly darker and with small metallic medial green spot on transverse submarginal ridge of sternum 4. (23) *Genitalia* (Figs. 186, 210) with apex of apical stylus on gonostylus enlarged like bowl of spoon. Ventral lobe large, with fringe of hairs on lower margin.

FEMALE (Figs. 8, 10, 12, 14, 16)

General coloration of head, mesosoma and metasoma bright green to blue-green. **Head:** pubescence as in *A. viequesensis.* (1) *Labrum* as in *A. hispaniolicus.* (2) *Clypeus* with broad, deep punctures on brown-black portion becoming deeply rugose on upper ½. (3) *Interocular area* deeply rugose, with rugae largest just above antennal sockets; supraclypeal protuberance rugose. (4) *Vertex* finely rugose anteriorly, becoming coarsely rugose laterally and posteriorly. (5) *Gena* with less than ten extremely large rugae extending postero-dorsally from antero-ventral margin (Fig. 16). (6) *Malar area* as in *A. viequesensis.* (7) *Mandible* as in *A. viequesensis* but with basal area darkened and with metallic basal spot. (8) *Antenna* brown-black, slightly paler on underside of flagellum, apex of apical flagellomere sometimes conspicuously paler than other flagellomeres. **Mesosoma** (Figs. 8, 10, 12, 14): with pubescence as in *A. viequesensis.* (9) *Pronotum* with lateral angle and posterior lobe slightly angular; dorsal portions of lateral angle and posterior lobe rugose and separated from lower portion by distinct carina extending from lateral angle to posterior lobe; postero-lateral area with 3-6 strong horizontal carinae. (10) *Mesoscutum* very coarsely rugose laterally and anteriorly, becoming coarsely and contiguously punctate medially and posteriorly. (11-12) *Mesoscutellum* and *metanotum* as in *A. viequesensis.* (13) *Mesepisternum* evenly, extremely deeply and coarsely rugose. (14) *Metepisternum* with extremely coarse horizontal carinae. (15) *Propodeum* with very strong propodeal carina; propodeal shield with strong carinae extending dorso-laterally from medial groove; dorsal area with extremely coarse carinae extending postero-laterally from antero-dorsal margin; lateral area with coarse, anastomosing carinae extending from metepisternum to lateral portion of propodeal carina. (16) *Wing* as in *A. viequesensis* but with veins darker. (17) *Tegula* as in *A. viequesensis* but with amber replaced by dark brown, metallic tints slightly more extensive, and yellow band largely or wholly obscured. (18-20) *Fore, middle* and *hind legs* dark brown with coxae wholly to partially covered with bright metallic green (least on middle coxa); pubescence as in *A. viequesensis* but darker (almost black) dorsally on middle tibia, hind tibia and apex of hind femur. **Metasoma:** (21) *Terga* as in *A. viequesensis* but with central brown bands absent or very faint. (22) *Sterna* dark brown with strong metallic tints on all or most of exposed portions; pubescence as in *A. viequesensis.*

Agapostemon radiatus (Say)

Halictus radiatus Say 1837. Type probably destroyed.
Agapostemon pulchra Smith 1853. Type ♂, British Museum (Natural History).
Agapostemon sulcatulus Cockerell 1909. Type ♂, U.S. National Museum.

The type of *Halictus radiatus* has probably been destroyed, but the description leaves no doubt of its identity. Michener has examined the type of *Agapostemon pulchra* (which is not labeled "California" as reported by Sandhouse, 1936) and I have examined the type of *Agapostemon sulcatulus*.

DISTRIBUTION (Fig. 18). Specimens have been collected as far north as Treesbank, Manitoba; as far south as Orange Co. in central Florida; as far east as Cape Cod, Massachusetts; and as far west as Sioux Co., Nebraska. In the northern part of the range (Wisconsin) females have been collected from April through October and males from July through October. In the central part of its range (Kansas) females have been collected from April through November and males in April and July through November. In the southern part of its range females have been collected from April through September and males from June through August and in October. Most abundant at elevations of less than 2,000 ft. (610 m), *A. radiatus* has been collected as high as 4,100 ft. (1,250 m) in the Smoky Mountains of North Carolina.

DIAGNOSIS. The male may be distinguished from many species by the yellow maculations on its 6th metasomal sternum and by the tooth on its hind femur; from *A. melliventris* by the brown-black on the anterior surface of its first metasomal tergum; from *A. texanus* and *A. angelicus* by its lack of conspicuous metallic tints on metasomal tergum 4, and by its lack of a broad, subapical, transverse ridge on metasomal sternum 4; and from males of *A. splendens, A. cockerelli* and *A. femoratus* by its unmodified hind basitarsus. The female may be distinguished from many species by its metallic green metasomal terga; from *A. texanus* and *A. angelicus* by its coarsely punctate or rugose mesoscutum without punctures of two distinct sizes; from *A. splendens* by its smaller size, coarse parallel carinae dorsomedially on its propodeum, its bright yellow mandibles (ferruginous apically), and its very pale amber to clear wings; from *A. femoratus* by its mesoscutum (coarsely punctate with rugae anteriorly and laterally in *A. radiatus*, almost entirely coarsely rugose in *A. femoratus*). The female cannot be morphologically differentiated from females of *A. cockerelli* but may be distinguished by its eastern distribution.

DESCRIPTION

MALE (Figs. 105-106, 161)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma with black and yellow bands. **Head** (Figs. 105-106):

pubescence white, pale yellowish on interocular area, becoming pale amber on vertex. (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with large scattered punctures below, becoming weakly rugose above. (3) *Interocular area* with very deep, fine, contiguous punctures below vertex, becoming weakly and finely rugose at level of and below antennal sockets; supraclypeal protuberance rugose. (4) *Vertex* finely and deeply punctate below ocelli and laterally, becoming deeply rugulose behind and between ocelli. (5) *Gena* with short, weak, parallel, well separated carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* bright yellow; very short. (7) *Mandible* bright yellow with apical ¼-⅓ dark ferruginous. (8) *Antenna* brown-black above with apical ½ of apical flagellomere amber; underside of flagellum amber to pale amber; underside of scape and pedicel bright yellow (underside of pedicel sometimes brown). **Mesosoma:** pubescence white, becoming yellowish to fuliginous on mesonotum and metanotum. (9) *Pronotum* with distinctly, but not acutely, angular lateral angle and posterior lobe; distinct carina extending postero-ventrally from lateral angle; distinct vertical carina laterally; and numerous weak horizontal carinulae. (10) *Mesoscutum* with fine, deep, contiguous punctures becoming rugose antero-laterally. (11) *Mesoscutellum* with fine, deep, contiguous punctures medially, becoming scattered in shiny lateral area. (12) *Metanotum* finely but deeply rugulose. (13) *Mesepisternum* moderately deeply and moderately coarsely rugose anteriorly, becoming slightly less deeply and coarsely rugose posteriorly. (14) *Metepisternum* moderately deeply and moderately coarsely rugose. (15) *Propodeum* with strong propodeal carina; propodeal shield moderately deeply and moderately coarsely rugose; dorsal area with short, coarse, parallel carinae extending postero-laterally from anterior margin, becoming moderately deeply and moderately coarsely rugose posteriorly (entire dorsal area rugose on some specimens); coarsely rugose postero-laterally, becoming punctate or finely rugulose antero-laterally. (16) *Wing* very pale brown, slightly darker on distal margin; veins and pterostigma pale brown, radial vein very dark brown. (17) *Tegula* amber with metallic tints antero-basally, with yellow on posterior margin, and with yellow submarginal band anteriorly. (18) *Fore leg* yellow; coxa metallic green and with small brown stripe posteriorly on tibia; pubescence yellowish to amber. (19) *Middle leg* with coloration and pubescence like fore leg with small, brown, subapical spot dorsally on femur and with brown posterior stripe on tibia larger. (20) *Hind leg* (Fig. 161) with coxa metallic green; trochanter brown to amber with yellow on apical ½ of lower side (extending to base on some specimens); femur yellow with brown spot dorsally at apex and sometimes posteriorly at base (much smaller than apical spot); tibia yellow with small brown to amber spot apically on anterior surface, with brown stripe antero-dorsally often connected with brown basal spot;

tarsus yellow, basitarsus lacking basal ridge and apical groove. Pubescence yellowish to amber. **Metasoma:** (21) *Terga* black with yellow bands on basal halves of terga 2-6 and centrally on tergum 1; ventro-lateral margins of terga 1-6 transparent amber; and sometimes with faint metallic tints anteriorly on tergum 1 and postero-laterally on tergum 3. Pubescence dorsally on terga 1-4 very short and inconspicuous, pale on yellow bands, dark on brown bands; moderately long, yellowish pubescence anteriorly on tergum 1 and laterally on terga 1-4; moderately long and dark brown dorsally and laterally on terga 5-7. (22) *Sterna* yellow with narrow brown band on distal margin of sternum 2 pale and slightly broadened medially, becoming progressively darker and larger on sterna 3-5; sternum 6 with brown medial stripe varying from very narrow to ½ width of sternum; sternum 1 metallic green basally. Broad, low, transverse, subapical (not apical as in *A. texanus* and *A. angelicus*) ridge on sternum 4, most prominent laterally, and often with faint metallic tints medially; moderately long scattered hairs on exposed areas, 2-4 large stout bristles disto-laterally on sternum 4. (23) *Genitalia* indistinguishable from those of *A. femoratus*.

FEMALE (Figs. 55-56)

General coloration of head, mesosoma and metasoma bright metallic green to blue-green. **Head** (Figs. 55-56): pubescence white, becoming pale yellowish amber on vertex and, commonly, on interocular area. (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with punctures deep, scattered below, becoming subcontiguous and interspersed with weak horizontal rugae above. (3) *Interocular area* with coarse, deep, contiguous punctures dorso-medially, becoming moderately rugose laterally and ventrally; supraclypeal protuberance sparsely punctate and with weak horizontal carinae. (4) *Vertex* with coarse, deep, contiguous punctures anterior to ocelli, becoming more shallowly punctate or finely rugulose laterally; shallowly and finely rugose posteriorly and between ocelli. (5) *Gena* with moderate to coarse, contiguous, parallel carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* dark amber to dark brown; very short, nearly absent. (7) *Mandible* yellow with apical ½-⅓ dark ferruginous. (8) *Antenna* brown-black with underside of flagellum very slightly paler than upperside. **Mesosoma:** pubescence white, becoming slightly yellowish to fuliginous on mesonotum and metanotum. (9) *Pronotum* as in ♂. (10) *Mesoscutum* with deep, contiguous, moderately large punctures becoming rugose anteriorly and antero-laterally. (11) *Mesoscutellum* with small subcontiguous punctures medially, becoming larger and scattered on shiny lateral area. (12) *Metanotum* finely and shallowly rugulose. (13) *Mesepisternum* deeply and coarsely rugose anteriorly, becoming slightly less coarsely and less deeply rugose posteriorly. (14) *Metepisternum* with even, parallel, horizontal

carinae anastomosing posteriorly (on some specimens becoming rugose posteriorly). (15) *Propodeum* with very strong and prominent propodeal carina; propodeal shield weakly rugose (rugae often absent on upper margin); dorsal surface with very coarse, irregular and anastomosing carinae extending posteriorly from anterior margin; postero-lateral margin with moderately coarse horizontal carinae, becoming much finer and weaker antero-laterally. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but slightly darker. (18-19) *Fore* and *middle legs* dark brown to brown-black with coxae metallic green and with antero-dorsal pale amber to yellowish areas apically on femora and basally on tibiae; pubescence white to pale fuliginous or amber. (20) *Hind leg* dark brown to brown-black with metallic tints dorsally on coxa; pubescence creamy, becoming amber posteriorly on tarsus and dark brown to brown-black dorsally on tibia. **Metasoma:** (21) *Terga* with very fine subcontiguous punctures on metallic regions; pubescence white, becoming brown-black on terga 5-6; terga 2-4 with narrow band of tomentum basally, otherwise largely devoid of hairs; moderately long hairs anteriorly on tergum 1, laterally on terga 1-5, and dorsally on terga 5-6. (22) *Sterna* brown to brown-black with metallic tints basally on sternum 1 and some specimens with very weak metallic tints on sternum 4; exposed areas with long, white, scattered hairs.

Agapostemon rhopalocera Smith

Agapostemon rhopalocera Smith 1853. Type ♂, British Museum (Natural History).

The type of this rare and peculiar species was examined at the British Museum by C. D. Michener. I know of only two additional specimens (males), both loaned to me by the British Museum.

Distribution. The holotype is from "Mexico." The other two males were collected in May, 1913-14 at Atoyac, Vera Cruz, Mexico. This town lies just 3.5 km ESE of Pico de Orizaba at an elevation of about 600 m (1,968 ft.). As well as this area has been collected, it is surprising that no more specimens have been collected in the past 50 years. Perhaps the habitat of this species has been destroyed by human activities.

Diagnosis. The male may easily be distinguished from all other members of *Agapostemon* by its long filamentous flagellum with the apical flagellomere flattened (Fig. 131).

Description

male (Figs. 77-78, 131, 154, 207)

General coloration of head and thorax metallic green, abdomen with black and yellow bands. **Head** (Figs. 77-78): (1) *Labrum* as in *A. texanus* but slightly more acute apically. (2) *Clypeus* with punctation as in *A. leunculus,* pubescence white to yellowish. (3) *Interocular area* above an-

tennal sockets very coarsely rugose or with dense contiguous punctures, coarsely rugose at level of antennal sockets, becoming moderately rugose below antennal sockets; pubescence white to yellowish. (4) *Vertex* with sculpturing as in *A. leunculus;* pubescence white to yellowish. (5) *Gena* with sculpturing as in *A. leunculus;* pubescence white to yellowish as in *A. leunculus* but denser and medially more coarsely branched and bent medially so as to cover the proboscidial fossa. (6-7) *Malar area* and *mandible* as in *A. texanus.* (8) *Antenna* (Fig. 131) with apical flagellomere and distal ⅔ of subapical flagellomere dark brown to black, remainder of flagellum and pedicel brown above and yellow-amber below, scape amber with dark streak on distal ⅔ of upper surface. **Mesosoma:** pubescence moderately long, evenly distributed (except pronotum), and whitish to amber as in *A. leunculus.* (9) *Pronotum* as in *A. leunculus.* (10) *Mesoscutum* finely and contiguously punctate, sometimes finely rugose anteriorly and laterally. (11) *Mesoscutellum* with punctures separated by about ½ their diameters, slightly coarser than those of mesoscutum and becoming rugulose laterally. (12) *Metanotum* finely rugulose medially becoming shallowly rugose laterally. (13) *Mesepisternum* as in *A. nasutus.* (14) *Metepisternum* rugose with few weak horizontal carinulae. (15) *Propodeum* as in *A. leunculus* but with more prominent propodeal carina. (16) *Wing* as in *A. leunculus.* (17) *Tegula* as in *A. nasutus* but with reduced yellow area. (18) *Fore leg* as in *A. leunculus* but more slender; pubescence white to amber. (19) *Middle leg* very slender; coxa dark brown to black, remainder of leg yellow with brown-black on all but anterior surface of trochanter and with brown-black stripe on basal ½-⅔ of posterior surface of tibia; pubescence white to amber. (20) *Hind leg* (Fig. 154) very slender, coxa metallic green, trochanter brown-black, remaining segments yellow with brown streak on posterior of femur and brown at base of tibia; pubescence white to amber. **Metasoma:** (21-22) *Terga* and *sterna* as in *A. leunculus.* (23) *Genitalia* (Fig. 207) very similar to *A. leunculus* but penis valves broader and flatter, medial plate of gonostylus longer and narrower; and ventral lobe smaller and not notched.

Agapostemon sapphirinus n. sp.

The name of this species refers to the sapphire blue color of the female.

I have seen 15 specimens (14 ♂, 1 ♀) of this species. The female holotype, the allotype and the 13 male paratypes are all labeled, "Bahamas/ Clarencetown/Long Isl. Febr//Utowana/Exp. 1934." All of the types are at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

DIAGNOSIS. Both males and females may be distinguished from all other West Indian species, except *A. cyaneus* and *A. ochromops,* by their milky to yellowish eyes and pterostigma. The male may be distinguished from

A. cyaneus by the pale amber to yellow on the underside of its pedicel, but cannot be reliably distinguished from *A. ochromops*. The female may be distinguished from *A. ochromops* by its dark purple metallic color and from *A. cyaneus* by its very coarsely carinate gena.

Description

male

General coloration of head and mesosoma bright metallic green to dark metallic green to blue, metasoma with black and yellow bands. **Head:** as in *A. viequesensis* but with eyes cream-colored, underside of flagellum yellower, pubescence of interocular area slightly yellow, and sculpturing very slightly coarser. **Mesosoma:** pubescence as in *A. viequesensis* but slightly yellowish laterally and slightly darker on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe more angular than in *A. viequesensis*. Carinulae on postero-lateral area larger and fewer in number than in *A. viequesensis*. (10-12) *Mesoscutum, mesoscutellum* and *metanotum* as in *A. viequesensis* but with very slightly coarser sculpturing. (13-15) *Mesepisternum, metepisternum* and *propodeum* as in *A. viequesensis* but with much coarser sculpturing. (16) *Wing* as in *A. viequesensis* but with yellow pigment on pterostigma and underside of larger veins. (17) *Tegula* as in *A. viequesensis* but with metallic tints less extensive. (18-20) *Fore, middle* and *hind legs* as in *A. viequesensis*. **Metasoma:** (21) *Terga* as in *A. viequesensis* but with metallic tints on some specimens (never as extensive as in *A. poeyi*), with dark bands almost black, and with yellow bands paler. Apex of pygidium nearly as acute as in *A. ochromops*. (22) *Sterna* as in *A. viequesensis* but often yellower basally and darker along apical margin. (23) *Genitalia* as in *A. poeyi* (cf. Figs. 186, 210).

female

Female as in *A. poeyi* but deep metallic blue, with metallic tints on sterna less intense and less extensive, with indistinct brown to ferruginous bands on terga 1-4, with creamy pigment on pterostigma and underside of larger wing veins, and with eyes pale.

Agapostemon semimelleus Cockerell

Agapostemon semimelleus Cockerell 1900. **Lectotype** ♂, Carnegie Museum, Pittsburgh.

Halictus (Agapostemon) andensis Vachal 1903 **(new synonymy).** Type ♀, Muséum National D'Histoire Naturelle, Paris.

? *Agapostemon castaneus* Schrottky 1902b. Type ♀? Departamento de Zoologia, São Paulo? Schrottky (1909b) tentatively synonymized the female of this species with *A. semimelleus*. Not having seen a type I cannot dispute his judgement.

? *Agapostemon coryliventris* Holmberg 1903. Type ♀.

? *Agapostemon multicolor* Holmberg 1903. Type ♂. According to J. S. Moure (pers. comm.) the types of most Holmberg species have been destroyed by dermestids. Therefore I am following Schrottky (1909b) in his synonymy of *A. coryliventris* and *A. multicolor* with

A. semimelleus. Although these nominal species may be synonyms of *A. chapadensis* they would still be junior synonyms.

I have seen the syntypes of *A. semimelleus* and have labeled the male as lectoholotype and the female as lectoallotype. Both specimens are from Chapada. I selected the male as lectoholotype because I am unable to distinguish the females of *A. semimelleus* and *A. chapadensis,* although the female lectoallotypes are easily distinguished.

DISTRIBUTION. This species is widespread in the *campos,* or tropical grasslands, of southern Brasil, of Paraguay and of northeastern Bolivia. It has also been collected at the heads of the Marañon and Ucayali Valleys in Peru, the heads of the Putamayo and Cauca Valleys in Colombia, and along the eastern slopes of the Andes in Bolivia and northern Argentina. It ranges from sea level in southeastern Brasil to 1,700 m in Bolivia. It has been collected during every month but May, but in the southern part of its range is found only during the summer months.

DIAGNOSIS. The male may be distinguished from most other South American species of *Agapostemon* by the acute lateral angle on its pronotum and lack of a "button" on its last visible sternum (6th). It may be distinguished from *A. chapadensis* by the shorter distal stylus of its genitalia (Figs. 173-174) and by the lesser amount of black on the posterior of its hind femur (Figs. 171-172).

The female cannot be distinguished from *A. chapadensis* (cf. VARIATION below) but it may be distinguished from other South American *Agapostemon* by the acute upturned flange on its anterior mesoscutal margin and lack of basal yellow bands on its metasomal terga.

VARIATION. When *A. semimelleus* and *A. chapadensis* were first described, the females were separated chiefly on the basis of metasomal color. Supposedly the female metasoma of *A. semimelleus* is honey-colored while that of *A. chapadensis* is black. However, I feel that this character is unreliable because I have seen specimens where the anterior of the metasoma was honey-colored while the posterior was black. I have also seen specimens with a dark brown metasoma.

Independent evidence leads me to believe that intra-specific variation masks interspecific differences between the females of these two species. The males of *A. semimelleus* are far more abundant and widespread than those of *A. chapadensis.* Unless one assumes that there are great disparities between the distributions and relative abundance of females and males, one must conclude that the metasoma of *A. semimelleus* females is frequently black. It is also possible that some females of *A. chapadensis* have brown or amber metasomas. At present there seems no solution to this problem. A similar problem exists with respect to the sculpturing of females of *A. texanus* and *A. angelicus.*

Description

male (Figs. 123-124, 171, 174, 220)

General color of head and mesosoma bright metallic green, metasoma banded with black and yellow. **Head** (Figs. 123-124): with pale amber pubescence on interocular area and vertex, becoming creamy on gena. (1) *Labrum* opaque yellow with apical and lateral margins transparent amber. Two-thirds as long as wide, apex narrowly rounded, basal ridge broad. Small, shallow, scattered punctures on dorsal ridge. Fringed with stiff submarginal bristles apically. (2) *Clypeus* with large (sometimes very large) scattered punctures on yellow region, becoming contiguously punctate to rugose on upper margin. (3) *Interocular area* with small to moderately small, deep, contiguous punctures below ocelli, becoming shallower and medium-sized at level of antennal sockets and still shallower below antennae; supraclypeal protuberance with large, contiguous, moderately deep punctures. Pubescence between antennal sockets ½-⅔ as long as scape, becoming shorter laterally, dorsally and ventrally and sub-tomentose ventro-laterally. (4) *Vertex* with deep contiguous punctures anteriorly and laterally, becoming shallower and slightly larger between ocelli and transversely carinate posteriorly. (5) *Gena* with parallel, subcontiguous, short carinae extending dorso-laterally from just behind smooth shiny area on antero-ventral margin. Pubescence postero-medially about as long as scape, becoming shorter anteriorly, laterally and dorsally. (6) *Malar area* yellow, very short and with minute appressed hairs. (7) *Mandible* yellow with apical ⅓ ferruginous. (8) *Antenna* brown to brown-black above, scape yellow below and sometimes with yellow extending dorsally at base, pedicel and flagellum amber to yellow below. **Mesosoma:** pubescence creamy to yellowish, becoming golden to fulvus on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe acutely pointed, lateral angle projecting antero-laterally; with conspicuous sharp carina extending postero-ventrally from apex of lateral angle; with weak irregular rugae postero-laterally. Pubescence above lateral angle and posterior lobe golden to fulvus, yellowish to creamy below. (10) *Mesoscutum* with large conspicuous flange laterally on anterior margin extending antero-dorsally; punctures small, very deep and contiguous, becoming rugose antero-laterally. (11) *Mesoscutellum* with lateral and medial punctures like that of mesoscutum, becoming larger and less dense laterally; area on each side of mid-line shiny with scattered punctures. (12) *Metanotum* coarsely punctate to rugose medially, becoming moderately coarsely rugose laterally. (13) *Mesepisternum* coarsely rugose anteriorly, becoming moderately coarsely rugose posteriorly. (14) *Metepisternum* moderately finely rugose with horizontal rugae longer and slightly more prominent than other rugae. (15) *Propodeum* with propodeal carina strong and conspicuous; propodeal shield very coarsely and deeply punctate to very

coarsely rugose; dorsal area very deeply rugose anteriorly and medially, becoming moderately rugose to coarsely punctate laterally; lateral area with small, deep, subcontiguous punctures anteriorly and centrally, becoming coarsely rugose adjacent to propodeal carina. (16) *Wing* hyaline or nearly hyaline, veins dark brown. (17) *Tegula* pale to dark transparent amber with broad submarginal yellow band anteriorly (partially obscured by pubescence) and yellow to dark brown on proximal margin. (18) *Fore leg* entirely yellow, or yellow with brown postero-proximally on tibia and postero-dorsally on distal ⅓ of femur. (19) *Middle leg* yellow with brown postero-dorsally on tibia, usually postero-dorsally at apex of femur, and occasionally on coxa. (20) *Hind leg* (Fig. 171) yellow with upper ½ of coxa metallic, with trochanter brown basally and sometimes amber apically, with brown apically on femur and antero-dorsally on tibia. **Metasoma:** (21) *Terga* 2-6 amber to brown-black on posterior ½ and yellow on anterior ½ (often partially concealed by overlap); tergum 1 varying from pale amber with brown band on posterior margin to brown-black with lateral yellow spot antero-dorsally, but most commonly intermediate in condition with antero-dorsal yellow band separating dark brown anterior and posterior regions. Very conspicuously punctate with subcontiguous punctures largest on tergum 1, becoming progressively smaller on posterior terga. Pubescence golden to fulvus anteriorly on tergum 1, laterally on terga 1-7 and dorsally on terga 5-7; very short dorsally on terga 1-4, golden to fulvus on yellow bands and dark brown to brown-black on dark bands. (22) *Sterna* 2-6 yellow but with amber to brown band at posterior margin of sterna 2-5, narrow on sternum 2, becoming progressively wider on successive sterna 3-5; sternum 1 amber with metallic tints basally. Sternum 6 with low proximo-medial ridge. Pubescence limited to scattered, moderately long, fulvus to golden hairs on exposed areas. (23) *Genitalia* (Figs. 174, 220) with very short ventral lobes bearing apical brush of large stiff hairs. Distal stylus little longer than width of medial plate.

FEMALE (Figs. 129-130)

General coloration of head and mesosoma bright metallic green, metasoma honey-colored to black. **Head** (Figs. 129-130): bright metallic green; pubescence white below becoming pale yellow above; sculpturing as in *A. atrocaeruleus*. **Mesosoma:** bright metallic green, but with tegula, legs and wing venation amber to brown; pubescence yellow or amber above, becoming creamy below; sculpturing as in *A. atrocaeruleus* but dorsal and lateral propodeal rugae more irregular. **Metasoma:** honey-colored to black; pubescence creamy, very short and appressed dorsally, becoming moderately long and erect anteriorly, laterally and posteriorly, and with narrow band of white tomentum basally on terga 2-4; sculpturing as in *A. atrocaeruleus*.

Agapostemon splendens (Lepeletier)

Halictus splendens Lepeletier 1841. Type ♀, Muséum National D'Histoire Naturelle, Paris.
Agapostemon aeruginosus Smith 1853. Type ♀, British Museum (Natural History).
Agapostemon splendens. Robertson, 1897.

I have seen the type of *Halictus splendens,* which was loaned to me by Dr. S. Kelner-Pillault. The type of *A. aeruginosus* was examined by Cockerell, and more recently by Michener, and both believe it is conspecific with *A. splendens.*

Distribution (Fig. 19). *Agapostemon splendens* is the most common species of *Agapostemon* in the southeastern United States and along the Gulf Coast. It is also common in the sandy areas of the Central States and Michigan. It is found as far south as Veracruz, Mexico, as far north as southern Saskatchewan, Canada, and as far west as south-central Utah. In Canada females have been collected in May, June, July and August; males in August and September. In Kansas females have been collected from April through October and males from July through October. In Florida both sexes have been collected every month of the year. While more common at elevations of less than 2,000 ft. (610 m), *A. splendens* has been collected as high as 6,600 ft. (2,012 m) in the Great Smoky Mountains National Park in Tennessee and 3,700 ft. (1,127 m) near Wray, Colorado.

Diagnosis. The male may be distinguished from other species by its toothed hind femora, the grooved basal ridge on its basitarsus, the apical stylus on its gonostylus, and its brown wings. The female may be distinguished from other species by its metallic green metasomal terga, rounded lateral pronotal angle, punctate mesoscutum and brown wings.

Description

male (Figs. 71-72, 166, 179, 200)

General coloration of head and mesosoma bright metallic green, metasoma with black and yellow bands. **Head** (Figs. 71-72): pubescence white, yellowish on vertex. (1) *Labrum* as in *A. texanus.* (2) *Clypeus* with large, shallow, scattered punctures on lower ½, becoming contiguous above. (3) *Interocular area* with deep, contiguous, medium punctures below ocelli, becoming rugose laterally and below; sculpturing of supraclypeal protuberance like that of adjacent clypeal area. (4) *Vertex* with deep, contiguous, medium punctures anteriorly, becoming rugose laterally, posteriorly and between ocelli. (5) *Gena* with short coarse carinae extending dorso-laterally from antero-ventral margin. (6) *Malar area* bright yellow, short. (7) *Mandible* bright yellow, pale ferruginous on apical ¼-⅓. (8) *Antenna* black above with yellow sometimes present on basal ¼-⅓ of scape and present on apical flagellomere; scape yellow below, pedicel with yellow spot on underside, and underside of flagellum pale amber. **Mesosoma:** pubescence

yellow to amber on mesonotum and metanotum, white elsewhere. (9) *Pronotum* with lateral angle rounded and rugose above; postero-lateral area with large vertical carina just anterior to several irregular horizontal carinae. (10) *Mesoscutum* with coarse contiguous punctures becoming rugose antero-laterally. (11) *Mesoscutellum* with coarse contiguous punctures anteriorly, becoming rugose posteriorly. (12) *Metanotum* rugose. (13) *Mesepisternum* coarsely rugose anteriorly, only slightly less coarse posteriorly. (14) *Metepisternum* with very coarse irregular horizontal carinae or coarsely rugose. (15) *Propodeum* with propodeal carinae distinct; propodeal shield coarsely rugose; very coarsely rugose postero-laterally, becoming rugulose antero-laterally; coarsely rugose dorsally with triangular medial area depressed, rugulose. (16) *Wing* yellowish brown, conspicuously darker on distal ¼-⅓; veins and pterostigma amber to brown with radius conspicuously darker than other veins. (17) *Tegula* pale transparent amber with green tints antero-basally and short transverse yellow band on anterior area curving rearward and almost reaching distal margin. (18) *Fore leg* yellow with coxa metallic green and trochanter with amber tints dorsally. (19) *Middle leg* yellow with metallic tints on coxa and dark brown streak centrally on postero-dorsal surface of tibia. (20) *Hind leg* (Fig. 166) yellow; coxa and trochanter metallic green; femur with brown on apical ¼-⅓ of anterior, dorsal and posterior surfaces; tibia with brown posteriorly on distal ½, antero-dorsally on proximal ½, basally, and apically on anterior and dorsal surfaces; basitarsus with amber on grooved portion of basal ridge and on apical groove. **Metasoma:** (21) *Terga* brown to brown-black with yellow bands on basal halves of terga 2-6, and with central yellow band on tergum 1; anterior face of tergum 1 pale amber to brown. Pubescence short, minute and dense on dorsal areas, brown-black on brown surfaces and white on yellow or amber surfaces; pubescence longer on anterior surface of tergum 1 and ventro-laterally on terga 5-7. (22) *Sterna* brown apically with varying amounts of yellow basally (always some yellow present); low, transverse, subapical ridge on sternum 4 (and sometimes 3) largest laterally; long, white, scattered pubescence on exposed areas. (23) *Genitalia* (Figs. 179, 200) with ventral lobes large and fringed with hairs distally.

FEMALE (Figs. 69-70)

General coloration of head, mesosoma and metasoma bright metallic green to blue-green. **Head** (Figs. 69-70): pubescence white to yellowish on clypeus and interocular area, becoming yellow to amber on vertex; white on gena. (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with large scattered punctures below, becoming subcontiguous on upper ⅔. (3) *Interocular area* rugose with coarse contiguous punctures below ocelli; supraclypeal protuberance with coarse punctures and faint horizontal carinae. (4) *Vertex*

with coarse contiguous punctures anteriorly, becoming rugulose laterally and between ocelli to rugose posteriorly. (5) *Gena* with coarse carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* very short, dark brown. (7) *Mandible* yellowish to amber with apical ⅓-½ ferruginous. (8) *Antenna* dark brown to brown-black with underside of flagellum slightly paler. **Mesosoma:** pubescence white, becoming yellowish on mesonotum and metanotum. (9) *Pronotum* with lateral angle rounded; dorsal aspect of lateral angle and posterior lobe shallowly rugose; postero-lateral area with several carinae extending postero-ventrally and antero-dorsally. (10) *Mesoscutum* with coarse, deep, contiguous punctures becoming rugose antero-laterally (punctures sometimes appearing to be of two sizes as in *A. texanus* but surface never as shiny). (11) *Mesoscutellum* with large scattered punctures and with much smaller contiguous punctures; central region just lateral to mid-line often shiny and devoid, or nearly devoid, of small punctures. (12) *Metanotum* rugose to rugulose. (13) *Mesepisternum* coarsely rugose. (14) *Metepisternum* rugose or with very irregular horizontal carinae. (15) *Propodeum* with strong propodeal carina; propodeal shield coarsely rugose or with irregular carinae extending dorso-laterally from medial groove. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but slightly darker amber. (18) *Fore leg* dark brown to brown-black; coxa metallic green; femur with pale yellow anteriorly, dorsally and posteriorly at apex; tibia with basal yellow spot dorsally and pale brown on anterior surface; tarsus pale brown; pubescence white to amber. (19) *Middle leg* like fore leg but with coxa largely brown and with pubescence brown-black dorsally on tibia and basitarsus. (20) *Hind leg* brown to brown-black, coxa with metallic tints dorsally; pubescence white to amber, becoming brown-black dorsally on tibia and basitarsus. **Metasoma:** (21) *Terga* bright metallic green to blue dorsally, becoming brown ventro-laterally and brown basally on tergum 1. Pubescence white, becoming black on terga 5-6; long ventro-laterally on anterior surface of tergum 1 and dorsally on terga 5-6; terga 2-5 with basal bands of white tomentum. (22) *Sterna* brown to brown-black with long white hairs scattered on exposed areas.

Agapostemon swainsonae Cockerell

Agapostemon swainsonae Cockerell 1910b. Type ♂, British Museum (Natural History).

The type has been examined by C. D. Michener. Its shiny mesoscutum leaves no doubt as to its identity.

The female is recognized here for the first time.

Distribution. This species is apparently limited to the island of Jamaica. I have seen specimens from the following localities: Yardley Chase, Santa Cruz Mtns., St. Elizabeth, 1,500 ft., (2 ♂, Oct.); Mandeville (1 ♂); Portland (2 ♀); Christina, 3,000 ft. (1 ♀, July); Hanover, Great River District (1 ♀, Jan.); Baron Hill, Trelawny (1 ♀, June).

DIAGNOSIS. The male is easily distinguished from all other West Indian species by its very shiny, weakly sculptured mesoscutum. The female has not been recognized previously owing to its similarity to *A. viridulus*. It may be distinguished from all but *A. viridulus* and *A. hispaniolicus* by its bright metallic green head and mesosoma and black metasoma; from *A. hispaniolicus* by its more rugose interocular area; and from *A. viridulus* by the lack of metallic green tints at the base of its mandibles and by the lighter color of its mandibles.

DESCRIPTION

MALE (Figs. 113-114, 147, 209)

General coloration of head and mesosoma bright metallic green and shiny, metasoma amber to yellowish brown. **Head** (Figs. 113-114): pubescence yellowish on clypeus, interocular area and vertex; white on gena. (1) *Labrum* as in *A. viridulus* but yellow to white on basal ½ and pale transparent amber on apical ½. (2) *Clypeus* yellow to white below and nearly as elongate as in *A. viridulus;* punctures scattered and with numerous transverse rugulae on metallic area; pubescence short and sparse. (3) *Interocular area* shallowly rugulose around antennal sockets, becoming finely and shallowly punctate dorsally and ventro-laterally; supraclypeal protuberance with punctures and transverse rugulae similar to those on clypeus; pubescence as in *A. viridulus*. (4) *Vertex* with very shallow, small, scattered punctures anteriorly and laterally, becoming finely rugose posteriorly; area between ocelli almost impunctate; pubescence as in *A. viridulus*. (5) *Gena* as in *A. viridulus* but with rugae weaker and more numerous. (6) *Malar area* as in *A. viridulus* but slightly shorter. (7) *Mandible* as in *A. viridulus*. (8) *Antenna* medium brown above, scape yellow to white below, flagellum amber to creamy below, underside of pedicel slightly darker than underside of flagellum. **Mesosoma:** pubescence creamy to yellowish on mesonotum and metanotum, white laterally, ventrally, and on propodeum. (9) *Pronotum* as in *A. viridulus*. (10) *Mesoscutum* very shiny (more so than in any other species of *Agapostemon*); very shallow, small punctures separated by their diameters. (11) *Mesoscutellum* very shiny with very small, shallow, widely scattered punctures. (12) *Metanotum* shiny, with minute, shallow, scattered punctures medially, becoming finely and irregularly rugulose laterally. (13) *Mesepisternum* as in *A. viridulus* but sculpturing finer and shallower. (14-15) *Metepisternum* and *propodeum* as in *A. viridulus* but with slightly shallower sculpturing. (16) *Wing* as in *A. viridulus* (1 ♂ with white pigment on underside of pterostigma and veins). (17) *Tegula* pale transparent, metallic tints absent or very faint, and yellow to creamy transverse lunule truncate basally and almost reaching distal margin. (18-19) *Fore* and *middle legs* yellowish amber with strong metallic tints on coxae; pubescence white on coxae, amber on other segments. (20) *Hind leg* (Fig. 147) as in

A. viridulus but with brown areas much paler brown (or amber). **Metasoma:** (21) *Terga* amber with indistinct, slightly darker bands centrally. Pubescence moderately long, scattered, white ventro-laterally and on anterior surface of tergum 1; very short, inconspicuous white tomentum basally on terga 2-6 (usually hidden by overlapping terga); inconspicuous, dense, short, prostrate hairs dorsally on terga 1-4; long fuliginous hairs dorsally on terga 4-7. (22) *Sterna* amber to yellowish with long, white, scattered hairs on exposed areas. (23) *Genitalia* as in *A. viridulus* but with only about ½ as many lateral grooves on gonocoxa (Fig. 209).

FEMALE (Figs. 35-36)

As described for *A. viridulus* but slightly bluer on head and metasoma; with finer sculpturing; with lower portion of clypeus, basal ⅔ of mandible, and labrum amber; and without metallic tints basally on mandible.

Agapostemon texanus Cresson

Agapostemon texanus Cresson 1872. Type ♀, Academy of Natural Sciences, Philadelphia.
Agapostemon texanus subtilior Cockerell 1898. Type ♀ (?), whereabouts unknown; **neotype** ♀, University of Colorado Museum, Boulder.
Agapostemon borealis Crawford 1901. Type ♀, Academy of Natural Sciences, Philadelphia.
Agapostemon californicus Crawford 1901. Lectotype ♀, U.S. National Museum.
Halictus (Agapostemon) brachycerus Vachal 1903 **(new synonymy).** Type ♂, Muséum National D'Histoire Naturelle, Paris.
Agapostemon texanus iowensis Cockerell 1910c **(new synonymy).** Type ♀, U.S. National Museum.
Agapostemon proscriptus Cockerell 1912b **(new synonymy).** Type ♀, U.S. National Museum.
Agapostemon joseanus Friese 1916 **(new synonymy).** Type ♀, Zoologisches Museum, Humboldt Universität, Berlin.
Agapostemon sulfuripes Friese 1916 **(new synonymy).** Type ♂, whereabouts unknown.
Agapostemon cyanozonus Cockerell 1924 **(new synonymy).** Type ♂, California Academy of Sciences, San Francisco.
Agapostemon proscriptellus Cockerell 1924 **(new synonymy).** Type ♀, California Academy of Sciences, San Francisco.
Agapostemon texanus vandykei Cockerell 1925. Type ♀, California Academy of Sciences, San Francisco.
Agapostemon californicus psammobius Cockerell 1937b **(new synonymy).** Type ♂, California Academy of Sciences, San Francisco.
Agapostemon angelicus idahoensis Michener 1937 **(new synonymy).** Type ♀, Snow Entomological Museum, University of Kansas, Lawrence.
Agapostemon californicus clementinus Cockerell 1939 **(new synonymy).** Type ♀, University of Colorado Museum, Boulder.

I have examined the types of all the nominal species and subspecies listed above except *A. texanus subtilior* and *A. sulfuripes.* As I find the females of *A. texanus* are indistinguishable from those of *A. angelicus*, female synonymies are based upon the distributions of the males (see map, Fig. 20). The type localities are as follows: *A. texanus,* Texas; *A. borealis,* Vancouver I., Canada; *A. californicus,* Pacific Grove, California; *H. (A.) brachycerus,* Guatemala; *A. texanus iowensis,* Ames, Iowa; *A. proscriptus,* Guatemala City, Guatemala; *A. joseanus,* San José, Costa Rica; *A. cyanozonus,*

Guaymas, Mexico; *A. proscriptellus,* Guaymas, Mexico; *A. texanus vandykei,* Yosemite Valley, California; *A. californicus psammobius,* San Miguel I., California; *A. angelicus idahoensis,* Challis, Idaho; *A. californicus clementinus,* San Clemente I., California.

The type of *Agapostemon texanus subtilior* Cockerell has not been identified by subsequent revisors and it is possible that Cockerell failed to designate the type series with appropriate labels. I have designated a female in the University of Colorado Museum as the **neotype.** This specimen is probably from the series described by Cockerell as it bears a label identical to that of some of the females mentioned by Cockerell, "Pasco, Wash/5 25 96."

I have not been able to examine a type of *Agapostemon sulfuripes* Friese, but the description is good and its identity with *A. texanus* is obvious.

DISTRIBUTION (Fig. 20). The range is greater than that of any other species in the genus. It may be found from southern Canada (52° N) to central Costa Rica (10° N) and from Cape Cod, Massachusetts (70° W) to Vancouver Island, Canada (125° W). *Agapostemon texanus* is most abundant on the western coast of the United States; fairly abundant in the United States west of the Mississippi River, except for the arid Southwest; uncommon in the arid Southwest, the United States east of the Mississippi River, Mexico, and Central America. This species occurs from sea level on the Atlantic, Gulf and Pacific coasts to about 8,000 ft. (2,438 m) in the Sierra Nevada of California. At the northern limits of its range (British Columbia) females of *A. texanus* have been collected from May through September and males from July through October; in Kansas females (including those of *A. angelicus*) have been collected from April through November and males in April (very rare) and from June through October; in Arizona females (including those of *A. angelicus*) have been collected from February through November and males in July and August; and in Mexico females (including those of *A. angelicus*) have been collected from February through October and in December, and males from April and June through September.

From its geographic distribution it appears that *A. texanus* is able to live under a wide variety of climatic conditions and in 70 of the 116 plant communities (see Appendix A) occurring in the United States (Küchler, 1964). Considering the lack of apparent climatic, biotic or edaphic factors correlated with its distribution, I find the distribution of *A. texanus* inexplicable. In a species as widespread and heterogeneous as this (cf. discussion of variation), factors which limit its distribution in one area may be relatively unimportant in another.

DIAGNOSIS. The male may be distinguished from males of many other species by its toothed hind femora, the apical stylus on its gonostylus, and

the lack of a low medial ridge on the apical ½ of its last visible sternum; from *A. splendens* by the lack of a grooved basal ridge on its hind basitarsus; and from *A. angelicus* by the apical stylus of its gonostylus (Figs. 180-181) and usually by the presence of a black stripe anteriorly on its hind tibia (if absent, then also lacking black stripe on posterior surface of hind tibia). The female may be distinguished from most other species by its bright metallic green to blue metasomal terga, its almost hyaline wings, and its two distinct sizes of mesoscutal punctures. I have not distinguished the females of *A. texanus* from those of *A. angelicus* except where they occur well outside the distribution of *A. angelicus* males (Fig. 20).

Variation. The amount of variation is reflected by the length of the synonymy, which consists of 15 names. Although specimens from different parts of the range differ in color, pattern and sculpturing, the male genitalia are all alike and there are intergrades among the other characters. Therefore, I conclude that the described variants all belong to one species. *A. angelicus* is superficially more similar to the typical form of *A. texanus* than is *A. texanus vandykei*. However, I regard *A. angelicus* as a separate species because: the male genitalia—which provide excellent specific characters in many other species of *Agapostemon*—are different from those of *A. texanus* (Figs. 180-181); there are no intergrades between the two species with regard to certain color patterns; the two are sympatric.

The variation within *A. texanus* falls into three major categories. These are the area and density of melanic pigmentation, the amount and hue of structural (metallic) coloration, and the sculpturing.

Melanic pigmentation is best seen in males, as it is obscured or replaced by the structural colors predominant in females. The melanic pigmentation varies in density from pale amber to brown-black, and varies both within and among localities. It was expected that there might be concordance of variation in the size of melanic maculations on the appendages. However, specimens from San Clemente Island, California have no yellow (0%) on either the fore coxa or lower ½ of the scape; whereas specimens from Jalisco, Mexico, have little (10%) yellow on the fore coxa but much (95%) on the lower ½ of the scape. Nor could precipitation, temperature or other ecological factors account for the similarity between, for example, populations from New Hampshire and San Clemente Island, California (underside of scape 100% black) or between Saskatchewan, Canada, and Missouri (underside of scape 100% yellow).

There are considerable differences of color pattern among various populations (Table 1). However, they can all be explained in terms of an increase or decrease in the amount (area) of melanic pigmentation. For example, although the black stripe on the posterior surface of the hind femur is absent in some populations and present in others, it can be shown that this

TABLE 1. Infraspecific variation among selected populations of *A. texanus*. Numbers represent range and modal class (italics). Structural colors from Ridgway (1912).

	POPULATIONS						
CHARACTERS	Mexico Jalisco	California San Clemente I.	California Trinity Co.	Washington Seattle	Canada Saskatchewan	New Hampshire	Missouri
Scape (% lower ½ dark) ♂ ♂	40–*5*–0	*100*	90–*20*–10	95–*20*–0	*0*	*100*–95	*0*
Fore coxa ♂ ♂ (% area dark)	100–*90*	*100*	90–*20*	70–*50*–40	40–*20*–0	*100*–95	60–*50*–40
Anterior stripe on hind femur of ♂ ♂ (% of femoral length)	*20*–0	95–*80*–70	30–*25*–20	40–*35*–10	30–*20*–0	95–*80*–50	90–*80*–45
Posterior stripe on hind femur of ♂ ♂ (% of femoral length)	*20*–0	*50*–40	10–*5*	50–*5*–0	*0*	100–*40*–30	100–*70*–50
Mesoscutum ♀ ♀ (Punctation)	Dull	Dull	Dull	Shiny	Shiny	Intermediate	Intermediate
Mesoscutum ♀ ♀ (Color of pubescence)	Yellow	Testaceous	Testaceous	Testaceous	White	Testaceous	Yellow
Structural colors ♀ ♀ (Ridgway, 1912)	Green b Cendre	G-BBk Paris Blue	G-Yi Javel Green	BB-Gi Ethyl Green	GB-Gi Viridian Green	Green b Cendre	GB-G Vivid Green

stripe is absent only in those populations in which the anterior stripe is reduced or absent, and that the reverse is never true. Every specimen in which the posterior hind femoral stripe is present and the anterior stripe absent proves, upon examination of the genitalia, to be *A. angelicus* rather than *A. texanus*. Therefore, although differences of color pattern do exist among individuals and populations, they are a result of the amount of melanic pigmentation.

One of the most obvious variables is the hue of the structural (metallic) coloration. It is usually pure green, but in some populations is yellowish or blue. The extremes of the yellowish and blue forms are so distinctive that they may be distinguished at a distance of several feet. The yellowish form *(A. vandykei)* occurs in the Sierra Nevada of California and in the Coast Ranges north of San Francisco. Limited to montane areas, it is not found along the coast or in the Central Valley. This form has strong brassy yellow overtones which are most striking in the Sierra Nevada south of Yosemite National Park and in the southern portion of the Coast Ranges north of San Francisco. The yellow cast becomes less pronounced further north to the point where it is replaced by the pure green of *A. texanus texanus* along the California-Oregon border.

The blue form of *A. texanus (A. californicus)* is found on the coast of California south of Cape Mendocino, in the Central Valley, and on the islands off the coast of southern California. It occurs only at low elevations and is not sympatric with the yellow form. It is most easily recognized by the bluish (rather than green) cast of the metallic coloration, which is particularly pronounced in the mesoscutum of males. This hue is most intense in the southern portion of the range, most notably on San Clemente Island *(A. californicus clementinus)*, where it is a very dark violaceous blue. However, it becomes greener further north to the point where, along the California-Oregon border, it is replaced by the pure green of *A. texanus texanus*.

It is interesting that there do not seem to be intermediates between the yellow and blue forms in the southern portions of their ranges. It would be logical to regard them as separate taxa were it not for the green intermediate forms to the north. Although the origins of this geographic distribution of color forms are doubtless environmental, the populations must be relatively homogeneous genetically for this character because annual or local environmental fluctuations have no apparent effect upon the colors of the populations.

Variation in sculpturing is best seen on the mesosoma of females. The punctures on the mesoscutum range from deep and contiguous (Fig. 24) to relatively shallow and far apart (Fig. 23). The former condition produces a rough and dull appearance, the latter a relatively smooth and shiny surface.

There are slight geographical variations in this character (Table 1), but the variation within a given locality is considerable. Although the rugae on the propodeum all follow the same general pattern, they vary considerably in number, coarseness, angle of divergence and number of interconnections (Figs. 25-26). This variability is so great within a locality that it is impossible to discern a significant difference among localities. In fact it is so great as to invalidate the contention of Sandhouse (1936) and her predecessors that *A. texanus* females may be distinguished from those of *A. angelicus* by propodeal sculpturing.

DESCRIPTION

MALE (Figs. 75-76, 165, 180, 201)

General coloration of head and mesosoma bright metallic green to blue, metasoma with black and yellow bands. **Head** (Figs. 75-76): (1) *Labrum* opaque lemon yellow with transparent pale amber margins (distal ⅔ amber on specimens from San Clemente I., California). Nearly as wide as long; distal margin rounded; and large transverse ridge on basal ⅓ with very slight medial depression. Punctures on crown of basal ridge shallow and separated by 2-3 times their diameters; submarginal punctures large and shallow medially, becoming smaller laterally and disappearing just anterior to basal ridge. Pubescence on crown of basal ridge minute, simple and erect; simple hairs in submarginal punctures about three times as long as puncture is wide and deflected distally. (2) *Clypeus* with coarse punctures contiguous at upper margin, becoming subcontiguous at lower margin and becoming smaller and shallower laterally; pubescence white, dense and about 2/5 length of clypeus medially, decreasing to 1/5 length of clypeus and loosely appressed at lateral margin. (3) *Interocular area* with small, deep, contiguous punctures below ocelli, becoming coarser laterally and moderately deeply rugulose above antennal sockets and shallowly rugulose ventro-laterally; supraclypeal protuberance coarsely punctate to shallowly rugose; pubescence white, erect, ½ as long as scape medially, becoming ¼ as long laterally. (4) *Vertex* with small, deep, contiguous punctures anteriorly, becoming shallower laterally; weakly rugose posteriorly, becoming weakly rugulose to weakly punctate between ocelli; pubescence white, ¾ as long as distance between lateral ocelli medially, decreasing to ½ as long as distance between lateral ocelli laterally. (5) *Gena* with hypostomal carina about 2.5 times as long as width of proboscidial fossa; short parallel carinulae extending postero-dorsally from antero-ventral margin; pubescence white, ranging in length from 2 5 as long as hypostomal carina centrally to 1/5 as long laterally and dorsally. (6) *Malar area* yellow to amber; very short; pubescence short, white, appressed. (7) *Mandible* opaque lemon yellow with distal ⅓ ferruginous; punctures few, shallow and scattered thinly over basal

½; pubescence scant with small patch of short white hairs on base of mandible. Row of approximately eight evenly spaced amber hairs along lower margin of basal ⅔ of mandible, with proximal hairs nearly twice as long as distal hairs. (8) *Antenna* brown to brown-black above with pale amber or yellow on apical ½ of apical flagellomere; flagellum pale amber below; scape and pedicel yellow to black below (see remarks on Variation). **Mesosoma:** pubescence white, becoming creamy to golden on mesonotum and metanotum; metallic coloration brassy green to blue. (9) *Pronotum* with lateral angle and posterior lobe slightly angular. Weak carina extending postero-ventrally from lateral angle; low carina extending postero-ventrally from center of lateral portion; weak horizontal carinulae near postero-lateral margin; long pubescence above lateral angle and posterior lobe and very fine white tomentum on postero-lateral area. (10) *Mesoscutum* with numerous small, dense, deep, contiguous punctures becoming rugose antero-laterally. (11) *Mesoscutellum* with punctation like that of mesoscutum but shallower, less dense, and often with shiny lateral area; pubescence like that of mesoscutum. (12) *Metanotum* coarsely punctate to rugulose; pubescence like that of mesoscutum. (13) *Mesepisternum* coarsely rugose anteriorly and only slightly less coarsely rugose posteriorly; pubescence long. (14) *Metepisternum* coarsely rugose, sometimes with horizontal rugae more prominent than others; pubescence long. (15) *Propodeum* with propodeal carina moderately weak to weak; propodeal shield moderately coarsely to moderately finely rugose; dorsal area moderately coarsely rugose medially and anteriorly, becoming finely rugose to finely rugulose postero-laterally; lateral area moderately finely rugose posteriorly, becoming punctate anteriorly. Pubescence very short dorsally, moderately long laterally and posteriorly. (16) *Wing* nearly hyaline, with pterostigma and all veins but radius amber; radius dark brown. (17) *Tegula* dark to very pale transparent amber, with large pale yellow lunulate maculation parallel to—but separated from—anterior margin, with metallic tints on basal margin, and with short pale yellow band on posterior margin. (18) *Fore leg* with coxa metallic green; trochanter yellow to brown-black; femur entirely yellow to yellow with dark brown on all but distal portion of posterior surface; tibia entirely yellow to yellow with dark brown on all but distal ⅓ of ventral surface and short brown stripe sub-basally on dorsal surface; tarsus yellow. Pubescence white, becoming pale amber on tarsus. (19) *Middle leg* with coxa brown-black tinted with metallic green; trochanter yellow with brown spot basally on posterior surface to entirely brown-black; femur entirely yellow to yellow with brown-black stripe broadest basally and narrowest distally extending from base to apex on posterior surface; tibia yellow with dark brown sub-basal stripe on basal ½ of dorsal surface to yellow with brown-black sub-basal stripe on basal ⅔ of dorsal surface and brown-black

stripe entire length of ventral surface; tarsus yellow. Pubescence similar to that on fore leg. (20) *Hind leg* (Fig. 165) with coxa bright metallic green; trochanter brown-black with metallic tints to yellow with dark brown basally; femur yellow with large brown apical spot postero-dorsally and sometimes with basal brown spot posteriorly; tibia yellow with small brown-black area at base and usually with apical streak of brown to brown-black on posterior surface and sub-basal streak of brown to brown-black antero-dorsally (posterior streak or both posterior and antero-dorsal streak may be absent); tarsus yellow. Basal ridge on basitarsus low and inconspicuous. Pubescence white, usually pale amber posteriorly on tarsus. **Metasoma:** (21) *Terga* black with yellow bands on basal halves of terga 2-5 and centrally on tergum 1; ventro-lateral margins of terga 1-6 transparent amber; metallic tints apically on terga 4-5, pygidium amber to yellow. Pubescence dorsally on terga 1-4 very short and inconspicuous, pale on yellow band, dark on brown-black bands; moderately long and white anteriorly on tergum 1, laterally on terga 3-5, and dorsally and laterally on terga 5-7. (22) *Sterna* yellow with brown band apically on sterna 2-5 (narrow on sternum 2 but occupying most of sternum 5); sternum 6 brown to yellow with brown band basally; sternum 1 yellow to amber, with metallic tints basally; sternum 4 with low, transverse ridge reaching distal margin laterally and usually with faint metallic spot medially. Moderately long, scattered, white hairs on exposed areas and with 2-4 large stout bristles disto-laterally on sternum 4. (23) *Genitalia* (Figs. 180, 201) with apical stylus, medial plate and basal stylus present; ventral lobe moderately large, fringed with short hairs distally.

FEMALE (Figs. 21-26, 67-68)

General coloration bright metallic green to blue or brassy. **Head** (Figs. 21-22, 67-68). (1) *Labrum* dark amber to ferruginous. Basal ridge prominent, proximal face sloping gently toward proximal margin, distal face sharply declivous, and apex of ridge with deep punctures; distal portion narrow, abruptly rounded at apex; conspicuous median keel on antero-distal portion, continued basally almost to basal ridge; anterior margin of keel flattened and slightly flared laterally; single row of dark amber, wide, flat, stiff bristles curving anteriorly at their apices and forming fimbria on antero-lateral margins of labrum. (2) *Clypeus* brown-black below, becoming green above; large, scattered, deep punctures below, becoming slightly smaller and subcontiguous above; pubescence creamy to amber with single row of amber bristles curving downwards from just above lower margin of clypeus. (3) *Interocular area* with deep, moderate sized, contiguous punctures below ocelli becoming rugose laterally and below; supraclypeal protuberance with moderate sized, scattered punctures between short transverse rugae. (4)

Vertex with deep, small to moderate sized, contiguous punctures anteriorly, becoming smaller and shallower laterally; rugulose posteriorly and between ocelli; pubescence creamy to amber. (5) *Gena* (Fig. 22) with regular, moderately coarse carinae extending postero-dorsally from antero-ventral margin; pubescence white and long. (6) *Malar area* amber to brown-black; very short; pubescence very short, sparse, white and tomentose. (7) *Mandible* yellow to pale amber with apical ⅓-½ ferruginous; moderately long, white, scattered pubescence at base and single row of moderately long amber pubescence on lower margin. (8) *Antenna* dark brown to brown-black with underside of flagellum amber. **Mesosoma:** pubescence white, becoming creamy to amber on mesonotum and metanotum. (9) *Pronotum* as in ♂ but with lateral angle and posterior lobe slightly more angular. (10) *Mesoscutum* (Figs. 23-24) with medium sized, moderately deep punctures separated by 2-3 times their diameters and interspersed with more numerous smaller and shallower contiguous to subcontiguous punctures; rugose antero-laterally (see discussion of Variation); pubescence moderately long. (11) *Mesoscutellum* with punctation like that of mesoscutum but small punctures smaller, more numerous and shallower; often shinier than mesoscutum; pubescence moderately long. (12) *Metanotum* finely and shallowly rugulose; pubescence moderately long. (13) *Mesepisternum* with coarse rugae anteriorly, becoming slightly less coarse posteriorly; pubescence moderately long. (14) *Metepisternum* with coarse, interconnected, horizontal carinae; pubescence moderately long. (15) *Propodeum* (Figs. 25-26) with prominent propodeal carina; propodeal shield weakly rugose with stronger rugae extending dorso-laterally from medial groove; dorsal area with weak, irregular, interconnected rugae extending posteriorly from anterior margin, becoming moderately finely rugose postero-laterally; lateral area with contiguous, horizontal carinulae and scattered small punctures; pubescence short dorsally, moderately long laterally and posteriorly. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but slightly darker amber. (18) *Fore leg* with coxa dark brown to brown-black and tinted with metallic green; trochanter dark brown to brown-black, often with narrow, inconspicuous, yellow band apically on posterior surface; femur brown to brown-black, with apical yellow band; tibia brown-black, with amber to yellow anteriorly; tarsus brown-black to pale amber; pubescence creamy on coxa, becoming amber on tarsus. (19) *Middle leg* similar in color to fore leg but with pubescence fuliginous dorsally on distal portion of tibia and amber ventrally on femur and tibia. (20) *Hind leg* with coxa dark brown to brown-black with strong metallic green tints dorsally; trochanter brown to brown-black; femur, tibia and tarsus brown-black to pale amber; pubescence creamy on coxa, trochanter and femur, becoming amber on tibia and tarsus and dark fuliginous to black on dorsal surface of tibia (darkest basally). **Metasoma:** (21) *Terga*

metallic green to blue or brassy; white bands of pruinose pubescence covering basal ⅓ of terga 1-4 and white, very short, simple hairs covering dorsal ⅔ of terga 1-4; terga 5-6 with long, dark brown to black pubescence. (22) *Sterna* brown to brown-black with metallic tints basally on sternum 1; long, creamy, scattered hairs on exposed areas.

Agapostemon tyleri Cockerell

Agapostemon tyleri Cockerell 1917a. Type ♀, U.S. National Museum.
Agapostemon martini Cockerell 1927, ♀ only, **(new synonymy).** Type ♀, California Academy of Sciences.

I have examined the holotypes of *Agapostemon tyleri* and *A. martini* and find them conspecific. Contrary to the opinion of Sandhouse (1936) I do not find the type of *A. tyleri* conspecific with that of *A. coloradensis* Crawford (cf. DIAGNOSIS). Cockerell correctly associated the sexes of *A. tyleri* but incorrectly associated the male of *A. cockerelli* with the female of *A. martini*. The male paratypes of *A. martini* are misidentified and belong to *Agapostemon cockerelli* Crawford.

DISTRIBUTION (Fig. 27). *Agapostemon tyleri* occurs in the desert Southwest and in arid parts of Mexico. I have seen specimens from as far north as Jerome, Arizona; as far south as Tehuacan, Puebla, Mexico; as far east as the Gulf Coast in Tamaulipas, Mexico; and as far west as Prescott, Arizona. It ranges from sea level in Tamaulipas, Mexico, to 8,200 ft. (2,499 m) at Pachuca, Hidalgo, Mexico. Throughout most of its range it occurs at altitudes of over 4,000 ft. (1,219 m) on the central plateau. In the United States males have been collected from February through April, June through September, and November; and females in April and May, July through September, and November. In Mexico males have been collected in February, May through September, and November; and females from June through September, and December.

DIAGNOSIS. The male may be distinguished from all North American species except *A. coloradinus* by the lack of yellow maculations on its dark brown to black metasomal sterna; from *A. coloradinus* by its smaller size, by the black streak extending the entire length of the posterior surface of its hind tibia (Figs. 159-160), and by its broader penis valve, which lacks conspicuous hairs on its dorsal crest (Figs. 226-227). The female may be distinguished from many other species occurring north of Mexico by its black metasoma and by the lack of yellow on its clypeus; from *A. virescens* by its finer genal carinulae (2-3 per 0.25 mm in *A. virescens* and 5-6 per 0.25 mm in *A. tyleri*, cf. Figs. 28-29); and from *A. coloradinus* by its colorless wings, darker tegulae, and shinier supraclypeal protuberance. This species is very close to *A. coloradinus*.

Description

male (Figs. 95-96, 159, 184, 198, 227)

General coloration of head and mesosoma bright metallic blue-green to blue, metasoma with black and pale yellow to creamy bands. **Head** (Figs. 95-96): pubescence snowy white. (1) *Labrum* as in *A. texanus* but more rounded at apex. (2) *Clypeus* as in *A. virescens* but punctures shallower and pubescence more dense. (3) *Interocular area* with coarse contiguous punctures (some specimens finely rugose around antennal sockets); supraclypeal protuberance as in *A. virescens*. (4) *Vertex* as in *A. virescens*. (5) *Gena* as in *A. virescens* but with carinae much finer. (6) *Malar area* yellow, never amber; short. (7) *Mandible* as in *A. virescens*. (8) *Antenna* as in *A. coloradinus*. **Mesosoma:** pubescence snowy white. (9) *Pronotum* as in *A. virescens* but with weaker sculpturing. (10) *Mesoscutum* as in *A. virescens* but with finer punctures and with anterior margin punctate. (11-13) *Mesoscutellum, metanotum* and *metepisternum* as in *A. virescens* but with finer sculpturing. (14-17) *Metepisternum, propodeum, wing* and *tegula* as in *A. coloradinus*. (18-20) *Fore, middle* and *hind legs* as in *A. virescens* but posterior surfaces of tibiae and femora nearly completely covered with dark brown to brown-black, and usually with small yellow rim apically on ventral surface of trochanters (Fig. 159). **Metasoma:** (21-22) *Terga* and *sterna* as in *A. coloradinus* but with creamy band on tergum 1 almost always broadly interrupted medially. (23) *Genitalia* (Figs. 184, 198, 227) as in *A. virescens* but with much smaller fold on medial plate of gonostylus and with prominent dorsal crest on penis valve.

female (Figs. 29, 51-52)

General coloration of head and mesosoma bright metallic blue-green, metasoma black with white hair bands. **Head** (Figs. 51-52): (1) *Labrum* as in *A. texanus*. (2-4) *Clypeus, interocular area* and *vertex* as in *A. virescens* but with center of supraclypeal protuberance shiny and nearly impunctate. (5) *Gena* as in *A. virescens* but with much finer and more numerous (5-6 per 0.25 mm) carinulae. (6) *Malar area* very dark ferruginous to brown-black; very narrow, almost absent. (7-8) *Mandible* and *antenna* as in *A. coloradinus*. **Mesosoma:** snowy white pubescence sometimes very slightly fuliginous on mesonotum and metanotum. (9-15) *Pronotum, mesoscutum, mesoscutellum, metanotum, mesepisternum, metepisternum* and *propodeum* as in *A. virescens* but with sculpturing slightly shallower and finer. (16) *Wing* as in *A. virescens* but always clear, never slightly amber. (17) *Tegula* as in *A. virescens* but dark amber (also darker than in *A. coloradinus*). (18-20) *Fore, middle* and *hind legs* as in *A. virescens* but with pubescence slightly paler. **Metasoma:** (21) *Terga* as in *A. virescens*

but with pubescence on 5-6 paler brown. (22) *Sterna* as in *A. virescens* but darker.

Agapostemon viequesensis Cockerell

Agapostemon viequesensis Cockerell 1918b. Type ♀, U.S. National Museum.
Agapostemon radiatus portoricensis Cockerell 1919 **(new synonymy).** Type ♂, U.S. National Museum.
Agapostemon portoricensis. Wolcott, 1948.

I have seen the types of both *A. viequesensis* and *A. radiatus portoricensis* and have no doubt that they are conspecific.

DISTRIBUTION. In addition to the types I have seen specimens from the following Puerto Rican localities: Aguada (1 ♂, 9 Nov.), Arecibo (4 ♀, 24-26 June; 1 ♂ & 7 ♀, 30 July-1 Aug.), Caguas (4 ♂, 28-29 May), Coamo Springs (2 ♂, 28 Dec.; 1 ♀, 29 Dec.), Dorado (1 ♂, 15 July; 1 ♀, 12 Apr.), Guayanilla (1 ♂, 22 July), Manati (2 ♂, 5 Mar.; 1 ♂, 7 June), Mayaguez (1 ♂, Mar.; 2 ♀, 21-23 June; 1 ♀, 16 Dec.), Ponce (1 ♂, Jan.), Puerto Cangrejos (1 ♂, 28 Jan.), Río Piedras (1 ♂, 23 Mar.), San Juan (3 ♂, 11-14 Feb.; 1 ♀, 14 Apr.; 1 ♂, 9-12 July), Vega Alta (1 ♀, 27 Oct.) and Mona Island (1 ♂ & 1 ♀, 21-26 Feb.; 2 ♂, Aug.). I have also seen specimens from Nassau, New Providence I. (1 ♂ & 2 ♀, 16 Dec.) and Arthurs Town, Cat I. (1 ♀, July-Aug.).

DIAGNOSIS. The male may be distinguished from *A. centratus* and *A. kohliellus* by its toothed hind femora; from *A. viridulus, A. obscuratus, A. hispaniolicus, A. swainsonae* and *A. cubensis* by its lack of an elongate clypeal region; from *A. cyaneus, A. sapphirinus* and *A. ochromops* by its lack of milky to yellowish eyes and pterostigma; from *A. insularis, A. jamaicensis* and *A. poeyi* by its lack of metallic green or blue medially on metasomal tergum 3; and from *A. columbi* by its lack of metallic green tints medially on metasomal tergum 3. The female may be distinguished from other West Indian species with metallic metasomas by its lack of milky to yellowish eyes and pterostigma and by the tints at the base of its mandible.

DESCRIPTION

MALE (Figs. 117-118, 145, 187, 224)

General coloration of head and mesosoma metallic blue-green, metasoma with brown-black and yellow bands. **Head** (Figs. 117-118): (1) *Labrum* yellow with apical margin transparent; basal ridge with very slight or no medial depression, apical ½ triangular; glabrous but for submarginal row of simple bristles. (2) *Clypeus* green above, yellow below; punctures scattered and small on yellow area, becoming larger and more numerous on green area; short white scattered hairs on green area almost absent from yellow area. (3) *Interocular area* blue-green above, becoming yellow-green below; rugose, becoming coarsely, deeply and contiguously punctate above

antennal sockets; pubescence yellowish to creamy, ¾ as long as scape between antennal sockets, becoming shorter laterally and ventrally, and becoming white and tomentose ventro-laterally. (4) *Vertex* with deep, contiguous, medium punctures anteriorly, becoming smaller and shallower laterally; rugose posteriorly, becoming irregularly rugulose between ocelli; pubescence as on interocular area but somewhat darker in color. (5) *Gena* with weak, fine, short rugulae extending postero-dorsally from antero-ventral margin; pubescence white, 1.5-2.0 times as long postero-medially as between antennal sockets but becoming shorter anteriorly, laterally and dorsally. (6) *Malar area* absent or very short. (7) *Mandible* yellow, apical ⅓ ferruginous; single row of bristles postero-ventrally, longest basally, becoming ⅓ as long distally. (8) *Antenna* with scape yellow, becoming dark brown to brown-black on distal ½-⅓ of upper surface; pedicel and flagellum dark brown to brown-black above, becoming pale amber to yellow below; apical flagellar segment yellow above and pedicel often slightly darker than flagellum. **Mesosoma:** pubescence wholly white or tinged with yellow on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe rounded; several to many fine, horizontal carinulae on postero-lateral area; pubescence on dorsal portions of lateral angle and posterior lobe as on mesoscutum, becoming very short, fine and inconspicuous on postero-lateral area. (10) *Mesoscutum* blue-green from above, yellow-green in oblique view; very finely and contiguously punctate, becoming rugose antero-laterally. (11) *Mesoscutellum* shinier than mesoscutum, with scattered large punctures interspersed with more numerous smaller and shallower punctures (faintly rugulose in some specimens). (12) *Metanotum* rugose. (13) *Mesepisternum* rugose anteriorly, becoming rugulose posteriorly and ventrally. (14) *Metepisternum* horizontally rugose. (15) *Propodeum* with distinct propodeal carina; coarsely rugose on propodeal shield, and posteriorly on dorsal portion, becoming moderately rugose antero-laterally; antero-dorsal margin with short rugae extending postero-laterally. (16) *Wing* transparent, slightly tinged with brown; radius brown-black, other veins and pterostigma brown. (17) *Tegula* pale transparent amber with metallic green tints antero-basally and yellow band almost reaching distal margin. (18-19) *Fore* and *middle legs* with coxae metallic green (only weakly tinted on middle leg), trochanters amber and remaining segments yellow with posterior of tibiae amber; pubescence pale amber. (20) *Hind leg* with coxa green, trochanter brown, femur yellow with brown dorsally on apical ⅓, tibia dark amber to brown dorsally, becoming yellow ventrally, tarsus yellow; pubescence amber (Fig. 145). **Metasoma:** (21) *Terga* with yellow band on basal ½ of dorsal areas; anterior portion of tergum 1 amber; anterior ½ of dorsal areas brown, darkest anteriorly and becoming transparent on posterior margin; terga 4-5 often with very faint metallic green

tints laterally. Apex of pygidium rounded (Fig. 224). Pubescence very minute, inconspicuous; white on yellow bands becoming brown on brown bands. Longer hairs white on anterior surface of tergum 1 and ventro-laterally on terga 2-5, and becoming brown dorsally on terga 5-7. (22) *Sterna* yellowish to amber or pale brown with metallic green tints basally on sternum 1. Sternum 4 with posterior margin slightly concave, and with low submarginal transverse ridge most prominent laterally; scattered white hairs on exposed areas. (23) *Genitalia* (Fig. 187) as in *A. poeyi* but apical stylus on gonostylus not as swollen at apex.

FEMALE (Figs. 9, 11, 13, 15, 17, 39-40)

General coloration of head, mesosoma and metasoma bright metallic green to blue-green. **Head** (Figs. 15, 17, 39-40): pubescence white, becoming fuliginous on vertex. (1) *Labrum* as in *A. hispaniolicus*. (2) *Clypeus* green above and brown to brown-black below; lower ½ with large punctures separated by at least their diameters, punctures on upper ½ slightly obscured by faint transverse rugae; pubescence sparse, white, longest dorsally, shortest and least abundant ventrally, row of long amber bristles on lower margin. (3) *Interocular area* with large, deep, contiguous punctures centrally on upper ⅓ becoming moderately rugose laterally and on lower ⅔; rugae nearest inner margins of compound eyes irregularly vertical in orientation. Pubescence ⅓-½ as long between antennal sockets as scape, becoming shorter ventrally and laterally. (4) *Vertex* with large, deep, contiguous punctures anteriorly and laterally, becoming rugose posteriorly and rugulose between ocelli. (5) *Gena* with fine carinulae extending dorso-laterally from antero-ventral margin; pubescence postero-medially twice as long as pubescence between antennal sockets, becoming shorter anteriorly, laterally and dorsally. (6) *Malar area* brown, very short to absent. (7) *Mandible* amber with apical ⅓ ferruginous; single row of hairs on postero-ventral margin long basally, becoming ⅓ as long distally. (8) *Antenna* brown-black above, slightly paler below; pedicel, proximal and distal flagellomeres often paler below than scape and remainder of flagellum. **Mesosoma:** (Figs. 9, 11, 13): pubescence white, becoming slightly fuliginous on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe rounded; postero-lateral area with 3-6 weak, horizontal carinulae; pubescence above lateral angle and posterior lobe like that on mesoscutum; lateral surface with very fine, inconspicuous, short, white hairs. (10) *Mesoscutum* with very fine, contiguous punctures, becoming shallowly rugulose antero-laterally. (11) *Mesoscutellum* with scattered large, deep punctures interspersed with far more numerous very small, shallow punctures. (12) *Metanotum* rugose. (13) *Mesepisternum* rugose with rugae finest posteriorly (specimens from Nassau, Bahamas with slightly coarser

sculpturing). (14) *Metepisternum* with regular horizontal carinulae. (15) *Propodeum* with strong propodeal carina; propodeal shield rugose or with irregular anastomosing rugae extending dorso-laterally from medial groove; dorsal area finely rugulose medially, laterally with anastomosing short carinae extending postero-laterally from anterior margin; lateral area with weak carinulae extending postero-dorsally from antero-lateral margin; pubescence very short and fine dorsally (absent medially), with long hairs posteriorly and laterally. (16) *Wing* as in ♂. (17) *Tegula* dark amber to brown with green tints antero-basally with faint (often obscure) yellow band almost reaching distal margin. (18-20) *Fore, middle* and *hind legs* with coxae dark brown; with metallic tints on anterior surface of fore coxa and dorsal surface of hind coxa; trochanters brown, remaining segments amber; pubescence white to pale amber, becoming dark brown dorsally on middle tibia, hind tibia and apex of hind femur. **Metasoma:** (21) *Terga* shiny metallic green with central brown band (varies greatly in size) devoid or nearly devoid of metallic tints; very fine, inconspicuous basal band of tomentum; medium length white to yellowish hairs ventro-laterally on terga 2-4 and anteriorly on tergum 1; long black hairs dorsally on terga 5-6. (22) *Sterna* amber to brown (faint metallic tints on specimens from New Providence I.); long white to yellowish, scattered hairs on exposed areas.

Agapostemon virescens (Fabricius)

Andrena virescens Fabricius 1775. Type ♀, British Museum (Natural History).
Andrena nigricornis Fabricius 1793. Types ♂, Zoologiske Museum, Copenhagen.
Halictus dimidiatus Lepeletier 1841. Type ♀, whereabouts unknown.
Halictus tricolor Lepeletier 1841 **(new synonymy).** Type ♂, Instituto e Museo di Zoologia, Universita di Torino, Italy.
Agapostemon bicolor Robertson 1893. Type ♀, Illinois Natural History Survey.

The synonymy of *Andrena nigricornis* Fabricius and *Halictus dimidiatus* Lepeletier with *Andrena virescens* Fabricius is based on their descriptions. C. D. Michener examined the type of *A. virescens* in the British Museum. G. C. Eickwort examined the type of *Agapostemon bicolor* in Urbana, Illinois, and confirmed Robertson's synonymy (1895) of this species with *A. virescens.* I have examined the type of *H. tricolor* and it is a synonym of *A. virescens,* not *A. radiatus* as stated by Sandhouse (1936).

Van der Vecht (1959) suggests that *Apis sericea* Forster (1771) may be a senior synonym of *A. virescens,* but the description given by Forster does not warrant such a conclusion (cf. *Nomina Dubia*).

Distribution (Fig. 30). Specimens have been collected as far east as Penobscot Co. in central Maine; as far west as Coos Co. on the Oregon Coast; as far south as Hernando Co. on the central western coast of Florida; and as far north as Vernon, British Columbia. This distribution is unusual inasmuch as it is wide, ranging from coast to coast, yet this species is com-

mon only from about 37° to 47° North latitude. In the northwestern part of the range (British Columbia and Alberta) males have been collected from August through October, and females from April through August and in October. In the central part of the range (Nebraska) males have been collected from July through October, and females from May through October. In the southeastern part of the range (Virginia, Tennessee, North Carolina and Georgia) males have been collected from June through September and in November, and females from May through August and in October. Although *A. virescens* occurs primarily at elevations of less than 2,000 ft. (610 m), I have seen specimens from as high as 4,000 ft. (1,219 m) on Middle Mountain, Virginia; 6,900 ft. (2,103 m) near Boulder, Colorado; and 7,000 ft. (2,134 m) near Salt Lake City, Utah.

DIAGNOSIS. The male may be distinguished from many other North American species by the lack of yellow maculations on its brown to brown-black sterna 5-6, by its medial ridge on the apical ½ of sternum 6 (last visible sternum), and by its gonostylus (Fig. 183); from *A. coloradinus* and *A. tyleri* by the restriction of brown to brown-black areas on the posterior surface of its hind leg to basal and apical regions of femur and tibia, and by its lack of a prominent dorsal crest on its penis valve. The females may be distinguished from other species occurring north of Mexico by its black metasomal terga and the lack of yellow on its clypeus; from females of *A. coloradinus* and *A. tyleri* by the coarser carinae on its gena (2-3 per 0.25 mm in *A. virescens,* 5-6 per 0.25 mm in *A. coloradinus* and *A. tyleri*), and its largely yellow mandibles (amber to brown in *A. coloradinus* and dark brown in *A. tyleri*).

DESCRIPTION

MALE (Figs. 97-98, 158, 183, 197)

General coloration of head and mesosoma bright metallic green, metasoma with black and yellow bands. **Head** (Figs. 97-98): pubescence white becoming yellowish to pale amber on vertex. (1) *Labrum* as in *A. texanus* but slightly blunter at apex. (2) *Clypeus* with medium size, shallow, scattered punctures on yellow portion, becoming more dense and slightly larger above. (3) *Interocular area* with large deep contiguous punctures below ocelli, becoming rugose and more shallowly sculptured below; supraclypeal protuberance shallowly rugose to punctate with few faint horizontal rugae. (4) *Vertex* with deep contiguous punctures anteriorly, becoming more finely punctate laterally, and coarsely but shallowly rugose posteriorly and between ocelli. (5) *Gena* with numerous short, parallel, subcontiguous carinae extending dorso-laterally from antero-ventral margin. (6) *Malar area* bright yellow to pale amber; short. (7) *Mandible* bright yellow with apical ⅓ ferruginous. (8) *Antenna* brown to brown-black above with shiny pale area on apical ½ of apical flagellomere; flagellum pale amber to brown

below; and underside of scape and pedicel yellow to largely black with yellow apically. **Mesosoma:** pubescence white, becoming pale amber to yellowish on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe neither very rounded nor acute; postero-lateral area with large, broad, low, vertical ridge just anterior to numerous very fine and faint carinulae. (10) *Mesoscutum* with fine contiguous punctures becoming finely rugose anteriorly and antero-laterally. (11) *Mesoscutellum* with punctures like those of mesoscutum but somewhat larger and less dense (especially laterally). (12) *Metanotum* finely and deeply rugose. (13) *Mesepisternum* coarsely rugose anteriorly, becoming finely rugose posteriorly. (14) *Metepisternum* with irregular horizontal carinae, anastomosing so as to appear largely rugose on some specimens. (15) *Propodeum* with distinct propodeal carina; propodeal shield coarsely and shallowly rugose; dorsal area coarsely rugose, postero-lateral area moderately rugose, becoming finely rugose to coarsely punctate antero-laterally. (16) *Wing* clear to transparent amber with apical regions slightly darkened. Radial vein dark brown, stigma and remaining veins pale brown. (17) *Tegula* pale transparent amber with green tints antero-basally, short transverse yellow band on anterior area curving rearward and almost reaching distal margin; posterior margin yellow. (18) *Fore leg* yellow with coxa bright metallic green; trochanter dark brown; femur with brown basally and postero-dorsally on basal ½ of tibia. Pubescence white to pale yellow. (19) *Middle leg* like fore leg but with only faint green tints on coxa and with brown streak postero-dorsally on basal ½-¾ of tibia. Pubescence white to pale yellow. (20) *Hind leg* (Fig. 158) with coxa bright metallic green; trochanter brown (sometimes with faint metallic tints); femur yellow with brown at base and apex; tibia yellow with brown at base (and sometimes at apex) and brown streak centrally on antero-dorsal surface. Pubescence white to pale yellow. **Metasoma:** (21) *Terga* brown to brown-black with yellow bands on basal halves of terga 2-5 and narrow yellow band centrally on tergum 1; pubescence white, short and appressed on dorsal portions of terga 1-4, moderate length elsewhere. (22) *Sterna* brown to brown-black with yellow basolaterally on sterna 2-4 (often hidden by overlapping sterna), and sternum 1 with metallic tints basally; apical ½ of sternum 6 with median ridge in shallow depression. Pubescence white and moderately long on exposed areas. (23) *Genitalia* (Figs. 183, 197) with dorsal crest of penis valve rounded and broad, not prominent as in most other species; ventral lobes of moderate size and distally fringed with hairs.

FEMALE (Figs. 28, 53-54)

General coloration of head and mesosoma bright metallic green to blue-green, metasoma black with white hair bands. **Head** (Figs. 28,

53-54): pubescence white, becoming faintly yellowish at vertex (and on interocular area of some specimens). (1) *Labrum* as in *A. texanus*. (2) *Clypeus* with large scattered punctures below, becoming contiguous above. (3) *Interocular area* with deep, medium sized punctures above, becoming deeply but finely rugose below. (4) *Vertex* with deep, small, contiguous punctures anteriorly, finer and shallower laterally and becoming finely rugose posteriorly; area between ocelli finely rugose to punctate. (5) *Gena* with moderately fine (2-3 per 0.25 mm) parallel carinae extending postero-dorsally from antero-ventral margin. (6) *Malar area* amber to ferruginous and very short, almost absent. (7) *Mandible* yellow or rarely very pale amber; with apical ½-⅓ ferruginous. (8) *Antenna* dark brown to brown-black with underside of flagellum slightly paler brown. **Mesosoma:** pubescence white, becoming pale amber to slightly fuliginous on mesonotum and metanotum. (9) *Pronotum* with lateral angle and posterior lobe neither very rounded nor acute; numerous very faint parallel carinulae extending antero-dorsally from postero-ventral area. (10) *Mesoscutum* with deep, medium sized, contiguous punctures becoming rugose anteriorly and antero-laterally. (11) *Mesoscutellum* with fine contiguous punctures medially, becoming large and separated by as much as 2-3 times their diameters laterally. (12) *Metanotum* rugulose. (13) *Mesepisternum* coarsely rugose, only very slightly finer rugae posteriorly. (14) *Metepisternum* with moderately coarse carinae regular and parallel anteriorly, irregular and anastomosing posteriorly. (15) *Propodeum* with prominent propodeal carina; propodeal shield with numerous weak carinae extending laterally and slightly dorsally from median groove; dorsal area with irregularly anastomosing carinae extending postero-laterally from anterior margin; lateral area with anastomosing horizontal rugae coarse posteriorly, becoming fine anteriorly. (16) *Wing* as in ♂. (17) *Tegula* as in ♂ but slightly darker. (18-20) *Fore, middle* and *hind legs* brown to brown-black with yellow dorsally at apex of femur and base of tibia of fore and middle legs; dorsal surface of hind coxa with strong metallic tints; pubescence white to amber, becoming fuliginous apically on dorsal surface of middle leg and brown-black basally on antero-dorsal surface of hind leg. **Metasoma:** (21) *Terga* black; white tomentose hair bands basally on terga 2-4 and centrally on tergum 1 (often broadly interrupted medially); pubescence anteriorly on tergum 1 and laterally on terga 1-5 white and moderately long; pubescence dorsally on terga 5-6 moderately long and brown to black. (22) *Sterna* brown to brown-black with long, scattered white hairs on exposed areas.

Agapostemon viridulus (Fabricius)

Apis viridula Fabricius 1793. Type ♀, Lund collection, Zoologiske Museum, Copenhagen.
Andrena (Agapostemon) femoralis Guérin-Méneville 1844. Type ♂, Museo Civico di Storia Naturale di Genova, Genoa.

Agapostemon semiviridis Cresson 1865 **(new synonymy).** Type ♀, Academy of Natural Sciences. Philadelphia.
Agapostemon viridulus. Dalla Torre, 1896.

J. S. Moure has selected a lectotype of *Apis viridula* and redescribed it (Moure, 1960). C. D. Michener has examined the type of *Andrena (Agapostemon) femoralis,* and I have examined the lectotype of *Agapostemon semiviridis.* I have no doubt that all three are conspecific. It should be noted that owing to the inadequacy of the original description *Agapostemon viridulus* was believed by many authors to be a synonym of *Agapostemon virescens.*

Except for the coloration of the head and thorax this species is indistinguishable from *Agapostemon obscuratus* Cresson. Sympatry and the absence of intermediate forms lead me to conclude that *A. obscuratus* is not conspecific with *A. viridulus.*

Distribution. I have seen specimens from the following localities in Cuba: Baracoa (3 ♂, Aug.), Castillo de Juaga, Cienfuegos (8 ♀, 4-5 Sept.), Central Jaronu (4 ♂, 31 Mar.), Cristo (4 ♂, 3 Oct.), Guane (2 ♂ & 1 ♀, 24-26 Sept.), Guantanamo (5 ♂ & 1 ♀), Havana (8 ♂), Puerto Baniato, Santiago de Cuba (1 ♂, Nov.), Río Toa, Baracoa (2 ♂, 26 Apr.), San Blas (1 ♂, 12 Aug.), Santiago de las Vegas (1 ♀, 10 Feb.), Siboney (1 ♀, Feb.), Soledad (1 ♂, 27 Feb.; 1 ♂, 4 Mar.; 1 ♂, 5 May), Trinidad Mts. (1 ♀, 28 Aug.), Vinales (2 ♀, 16-22 Sept.).

Diagnosis. The male may be distinguished from West Indian species, except *A. obscuratus* and *A. hispaniolicus,* by its black metasomal terga; from *A. obscuratus* by its bright metallic blue-green head and mesosoma; from *A. hispaniolicus* by the subcontiguous punctures of its mesoscutum. The female may be distinguished from West Indian species, except *A. obscuratus, A. hispaniolicus* and *A. swainsonae,* by its black metasomal terga; from *A. obscuratus* by its bright metallic blue-green head and mesosoma; from *A. swainsonae* by the metallic green tints on the base of its mandible; and from *A. hispaniolicus* by the coarser sculpturing of its interocular area.

Description

male (Figs. 111-112, 150, 178, 208)

General coloration of head and mesosoma metallic green to blue-green, metasoma dark brown to black. **Head** (Figs. 111-112): (1) *Labrum* yellow to white on basal ½, amber to brown on apical ½; apex smoothly rounded (not acute), basal ½ with shallow depression medially on transverse ridge; shiny and impunctate; pubescence limited to about 20 subapical bristles. (2) *Clypeus* yellow to white below and extraordinarily elongate; punctures coarse and scattered, weak transverse rugae medially on upper ½; pubescence short, sparse and white. (3) *Interocular area* with contiguous

punctures below median ocellus, becoming rugose midway between median ocellus and antennal sockets, rugosity at level of antennal sockets changing to scattered punctures ventro-laterally; supraclypeal protuberance with coarse scattered punctures and transverse medial rugae; pubescence white, nearly as long between antennal sockets as scape, becoming shorter laterally, dorsally and ventrally; ventro-lateral area near malar space with short, sparse, white tomentum. (4) *Vertex* with fine, contiguous punctures anteriorly and laterally, becoming rugose posteriorly; area between ocelli sparsely punctate; pubescence white, fuliginous between ocelli. (5) *Gena* with fine parallel rugae running postero-dorsally from antero-ventral margin; pubescence white and about 1.5 times as long postero-medially as pubescence between antennal sockets, becoming shorter laterally, anteriorly and dorsally. (6) *Malar area* yellowish, more than ½ as broad as long; shiny and impunctate; pubescence sparse, appressed, short and white. (7) *Mandible* yellow to creamy, apical ⅓-¼ transparent ferruginous; simple hairs on postero-ventral margin of mandible longest basally, becoming ⅓ as long apically. (8) *Antenna* with scape brown-black above, yellow below; pedicel dark brown; flagellum brown-black above, paler brown below. **Mesosoma:** pubescence fuliginous on mesonotum and metanotum, white laterally, ventrally and on propodeum. (9) *Pronotum* with lateral angle and posterior lobe rounded; sculpturing inconspicuous. Pubescence postero-laterally very fine, short and inconspicuous; dorsally on lateral angle and posterior lobe similar in length and color to that of mesonotum. (10) *Mesoscutum* with very fine, deep, contiguous punctures, becoming rugulose antero-laterally. (11) *Mesoscutellum* shiny with large, scattered, central punctures, becoming finer and more numerous anteriorly. (12) *Metanotum* finely and irregularly rugulose with large, scattered punctures. (13) *Mesepisternum* coarsely to moderately rugose anteriorly, becoming finely rugose posteriorly. (14) *Metepisternum* finely and horizontally carinulate. (15) *Propodeum* rounded posteriorly; propodeal carina absent; fine, even, horizontal carinulae laterally and posteriorly (uppermost of these becoming stronger along upper margin of propodeal shield); dorsal area of propodeum with fine, even carinulae running postero-laterally from posterior margin of metanotum. (16) *Wing* transparent, faintly fuliginous; veins and pterostigma dark brown, radius almost black. (17) *Tegula* dark transparent brown with metallic green tints on basal margin and submarginally on anterior ⅓ and with very fine scattered punctures. (18) *Fore leg* dark brown with yellow to white on antero-ventral surface of femur, on all but posterior surface of tibia, and on tarsus; coxa metallic green; pubescence white proximally, becoming amber distally. (19) *Middle leg* similar in color and pubescence to fore leg but with white to yellow areas on femur and tibia reduced, and with tarsus amber to brown, coxa slightly metallic

green. (20) *Hind leg* (Fig. 150) with coxa largely metallic green to blue; trochanter brown with metallic tints; femur brown with yellow to white antero-ventrally, on basal ⅔ antero-dorsally, and posteriorly around large tooth; tibia brown with yellow to white ventrally and antero-ventrally (yellow sometimes very reduced or absent); tarsus brown to amber. Hind leg very swollen, especially femur; basal ridge on basitarsus very prominent, broad and concave; apical groove broad and delimited by strong carina; pubescence amber on tarsus, white on other segments. **Metasoma:** (21) *Terga* brown-black (pygidium somewhat paler) and shiny; with long, sparse, white pubescence becoming fuliginous around pygidium and with very short, moderately dense pubescence brown-black and inconspicuous, and with narrow, basal bands of white tomentum on terga 2-6 (often hidden by preceding terga). (22) *Sterna* not quite as dark as terga, sternum 1 with metallic green tints basally; with sparse white pubescence on exposed portions. (23) *Genitalia* (Figs. 178, 208) with penis valves smooth basally on dorsal surface, with large dorsal crest grooved at apex. Gonocoxa with numerous deep longitudinal grooves laterally; gonostylus with simple apical stylus; medial plate with small fold on antero-medial margin; ventral lobes large, curled posteriorly and with dense, short, simple pubescence marginally on posterior surface.

female (Figs. 33-34)

General coloration of head and mesosoma metallic green to blue-green, metasoma black with narrow bands of white tomentum. **Head** (Figs. 33-34): pubescence white, fuliginous on vertex, and amber on lower margin of clypeus and on mandibles. (1) *Labrum* (Figs. 34 A-C) brown, with large, broad, distal keel; basal area with rounded medial protuberance and sharply delimited from distal process by marginal carina; additional transverse carina present between base of distal process and outer margin of basal area. (2) *Clypeus* elongate and with broad, very shallow, subapical depression or flattened area; punctures very coarse, widely separated distally, becoming more numerous above; irregular transverse rugae often scattered on metallic area. (3) *Interocular area* rugose, becoming punctate at vertex; supraclypeal protuberance with scattered punctures and regular transverse rugae. (4) *Vertex* finely and densely punctate anterior to and lateral to ocellar triangle, becoming shallowly and weakly rugose posterior to ocelli; area between ocelli with fine, scattered punctures. (5) *Gena* with numerous, regular, contiguous rugulae running postero-dorsally from antero-ventral margin. (6) *Malar area* very short, almost non-existent. (7) *Mandible* dark ferruginous brown with metallic green tints at base. (8) *Antenna* brown-black, slightly paler on underside of flagellum. **Mesosoma:** pubescence as in ♂. (9) *Pronotum* with lateral angle and posterior lobe rounded; weak carina running postero-laterally downward from lateral angle. (10) *Mesoscutum*

with dense, fine punctures contiguous centrally, becoming separated by about ½ their diameters posteriorly and becoming finely rugulose anteriorly. (11) *Mesoscutellum* with scattered medium punctures interspersed with more numerous fine punctures anteriorly, and finely rugulose posteriorly and laterally. (12) *Metanotum* with very faint rugulae running postero-laterally from anterior margin. (13) *Mesepisternum* moderately rugose; rugae moderately prominent anteriorly, becoming finer posteriorly. (14) *Metepisternum* finely, horizontally carinulate, with carinulae more numerous and less prominent than on ♂. (15) *Propodeum* not rounded posteriorly and with definite propodeal carina; carinulae on lateral and dorsal areas similar to ♂; numerous parallel carinulae on propodeal shield running dorso-laterally from median groove. (16-17) *Wing* and *tegula* as on ♂. (18-20) *Fore, middle* and *hind legs* brown-black to amber; pubescence creamy to amber, fuliginous on dorsal surfaces of tibiae, dark brown to black adjacent to basi-tibial plate on hind leg; posterior tibial spur with 3-5 (usually 4) spatulate teeth. **Metasoma:** (21) *Terga* brown-black to black, anterior area of tergum 1 often brown to amber; dorsal surfaces finely granulose, not shiny; pubescence on ventro-lateral areas of terga 1-4 as well as on anterior surface of tergum 1 scattered, of moderate length and white; dorsal portions of terga with very numerous, minute, simple, brown-black hairs directed posteriorly; basal bands of white tomentum on terga 2-5 usually hidden by preceding terga but may be visible laterally; abundant long brown-black pubescence on terga 5-6. (22) *Sterna* brown to black with scattered, simple, long white hairs on exposed portions.

NOMINA DUBIA

In 1771, J. R. Forster described *Apis sericea* from North America. Van der Vecht (1959) has suggested that it is a senior synonym of *Agapostemon virescens* Fabricius 1775. Forster's very brief description is sufficient only to indicate that he had a male *Agapostemon*. Forster made no mention of characters of specific significance and, in the absence of the type, I can accord only the status of *nomen dubium* to *Apis sericea* Forster.

In 1903, J. Vachal described *Halictus (Agapostemon) chiriquiensis* from a single female. It would seem from the description to be either *A. nasutus* or *A. leunculus*. I requested the type but Dr. S. Kelner-Pillault was unable to find it in the Muséum National D'Histoire Naturelle in Paris. Therefore, I consider *Halictus (Agapostemon) chiriquiensis* a *nomen dubium*.

APPENDIX A

The following list of plant communities in which *Agapostemon texanus* and *A. angelicus* may occur was derived by superimposing distributions of these species on the vegetation map of Küchler (1964). Only those communities present in the United States are listed, as comparable vegetation maps do not exist for Mexico and Central America. The letter "T" preceding a community indicates records of *A. texanus,* "A" indicates *A. angelicus,* and "TA" indicates both species. The numbers are those assigned to the communities by Küchler.

As Küchler's map is based on potential vegetation, this list may be unrealistically large, with the bees actually living in disturbed areas with little, if any, semblance of the potential climax or subclimax vegetation.

T 1. Spruce—Cedar—Hemlock Forest *(Picea—Thuja—Tsuga)*
T 2. Cedar—Hemlock—Douglas Fir Forest *(Thuja—Tsuga—Pseudotsuga)*
T 3. Silver Fir—Douglas Fir Forest *(Abies—Pseudotsuga)*
T 5. Mixed Conifer Forest *(Abies—Pinus—Pseudotsuga)*
T 6. Redwood Forest *(Sequoia—Pseudotsuga)*
T 7. Red Fir Forest *(Abies)*
T 8. Lodgepole Pine—Subalpine Forest *(Pinus—Tsuga)*
T 9. Pine—Cypress Forest *(Pinus—Cypressus)*
T 10. Ponderosa Shrub Forest *(Pinus)*
T 11. Western Ponderosa Forest *(Pinus)*
T 12. Douglas Fir Forest *(Pseudotsuga)*
T 13. Cedar—Hemlock—Pine Forest *(Thuja—Tsuga—Pinus)*
T 14. Grand Fir—Douglas Fir Forest *(Abies—Pseudotsuga)*
A 15. Western Spruce—Fir Forest *(Picea—Abies)*
TA 17. Black Hills Pine Forest *(Pinus)*
TA 18. Pine—Douglas Fir Forest *(Pinus—Pseudotsuga)*
A 19. Arizona Pine Forest *(Pinus)*
A 20. Spruce—Fir—Douglas Fir Forest *(Picea—Abies—Pseudotsuga)*
A 21. Southwestern Spruce—Fir Forest *(Picea—Abies)*
TA 23. Juniper—Pinyon Woodland *(Juniperus—Pinus)*
T 29. California Mixed Evergreen Forest *(Quercus—Arbutus—Pseudotsuga)*
T 30. California Oakwoods *(Quercus)*
A 31. Oak—Juniper Woodland *(Quercus—Juniperus)*
TA 32. Transition between 31 and 37
TA 33. Chaparral *(Adenostoma—Arctostaphylos—Ceanothus)*
T 35. Coastal Sagebrush *(Salvia—Eriogonum)*
T 36. Mosaic of numbers 30 and 35
TA 37. Mountain Mahogany—Oak Scrub *(Cercocarpus—Quercus)*
TA 38. Great Basin Sagebrush *(Artemesia)*
A 39. Blackbrush *(Coleogyne)*
A 40. Saltbush—Greasewood *(Atriplex—Sarcobatus)*
TA 41. Creosote Bush *(Larrea)*
TA 42. Creosote Bush—Bur Sage *(Larrea—Franseria)*
TA 43. Palo Verde—Cactus Shrub *(Cercidium—Opuntia)*
TA 44. Creosote Bush—Tarbush *(Larrea—Flourensia)*
TA 45. Ceniza Shrub *(Leucophyllum—Larrea—Prosopis)*
T 47. Fescue—Oatgrass *(Festuca—Danthonia)*
T 48. California Steppe *(Stipa)*
T 50. Fescue—Wheatgrass *(Festuca—Agropyron)*
T 51. Wheatgrass—Blue Grass *(Agropyron—Poa)*
TA 53. Grama—Galleta Steppe *(Bouteloua—Hilaria)*
A 54. Grama—Tobosa Prairie *(Bouteloua—Hilaria)*
TA 55. Sagebrush Steppe *(Artemesia—Agropyron)*
A 58. Grama—Tobosa Shrub Steppe *(Bouteloua—Hilaria—Larrea)*
TA 59. Trans-Pecos Shrub Savanna *(Flourensia—Larrea)*
TA 60. Mesquite Savanna *(Prosopis—Hilaria)*

T 61. Mesquite—Acacia Savanna (*Prosopis—Acacia—Andropogon—Setaria*)
T 62. Mesquite—Live Oak Savanna (*Prosopis—Quercus—Andropogon*)
T 63. Foothills Prairie (*Agropyron—Festuca—Stipa*)
T 64. Grama—Needlegrass—Wheatgrass (*Bouteloua—Stipa—Agropyron*)
TA 65. Grama—Buffalo Grass (*Bouteloua—Buchloë*)
TA 66. Wheatgrass—Needlegrass (*Agropyron—Stipa*)
TA 67. Wheatgrass—Bluestem—Needlegrass (*Agropyron—Andropogon—Stipa*)
TA 68. Wheatgrass—Grama—Buffalo Grass (*Agropyron—Bouteloua—Buchloë*)
TA 69. Bluestem—Grama Prairie (*Andropogon—Bouteloua*)
A 70. Sandsage—Bluestem Prairie (*Artemesia—Andropogon*)
TA 71. Shinnery (*Quercus—Andropogon*)
T 74. Bluestem Prairie (*Andropogon—Panicum—Sorghastrum*)
TA 75. Nebraska Sandhills Prairie (*Andropogon—Calamovilfa*)
TA 76. Blackland Prairie (*Andropogon—Stipa*)
T 77. Bluestem—Sacahuista Prairie (*Andropogon—Spartina*)
T 81. Oak Savanna (*Quercus—Andropogon*)
T 82. Mosaic of numbers 74 and 100
T 84. Cross Timbers (*Quercus—Andropogon*)
TA 85. Mesquite—Buffalo Grass (*Prosopis—Buchloë*)
TA 86. Juniper—Oak Savanna (*Juniperus—Quercus—Andropogon*)
TA 87. Mesquite—Oak Savanna (*Prosopis—Quercus—Andropogon*)
T 88. Fayette Prairie (*Andropogon—Buchloë*)
T 95. Great Lakes Pine Forest (*Pinus*)
TA 98. Northern Floodplain Forest (*Populus—Salix—Ulmus*)
T 99. Maple—Basswood Forest (*Acer—Tilia*)
T 100. Oak—Hickory Forest (*Quercus—Carya*)
T 102. Beech—Maple Forest (*Fagus—Acer*)
T 104. Appalachian Oak Forest (*Quercus*)
T 106. Northern Hardwoods (*Acer—Betula—Fagus—Tsuga*)
T 109. Transition between numbers 105 and 106
T 110. Northeastern Oak—Pine Forest (*Quercus—Pinus*)
T 111. Oak—Hickory—Pine Forest (*Quercus—Carya—Pinus*)
T 113. Southern Floodplain Forest (*Quercus—Nyssa—Taxodium*)

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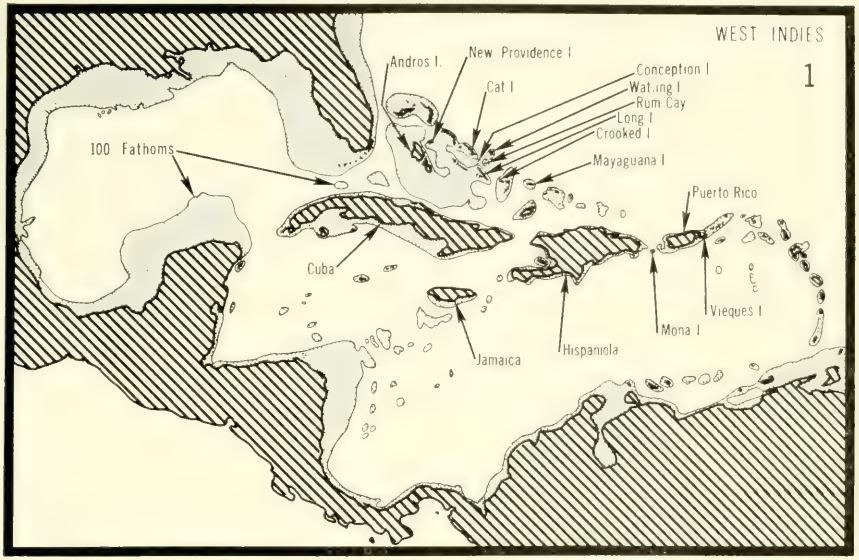


FIG. 1. Distributions of West Indian *Agapostemon* (stippled regions less than 100 fathoms in depth).

	Andros	New Providence	Cat	Conception	Watling	Rum	Long	Crooked	Mayaguana	Cuba	Hispaniola	Jamaica	Mona	Puerto Rico	Vieques	Costa Rica ?
poeyi	×	×	×	....	....	....	....	....	....	×	×	....	....	....	....	..
viequesensis	....	×	×	....	....	....	....	....	....	....	....	....	×	×	×	..
ochromops	....	×	×	×	....	×	....	....	×	..	....	....	....	....	....	..
columbi	....	....	....	....	×	....	....	....	....	....	....	....	....	....	....	..
sapphirinus	....	....	....	....	....	....	×	....	....	....	. .	....	. .	. .	....	..
cyaneus	....	....	....	....	....	....	....	×	....	. .	. .	....	....	....	....	..
insularis	....	....	....	....	....	....	....	....	....	....	×	....	....	....	....	..
jamaicensis	....	....	....	....	....	....	....	....	....	....	....	×	....	....	....	..
aenigma	....	....	....	....	....	....	....	....	....	..	....	....	....	....	....	?
viridulus	....	....	....	....	....	....	....	....	....	×	....	....	....	....	....	..
obscuratus	....	....	....	....	....	....	....	....	....	×	....	....	....	....	....	..
cubensis	....	....	....	....	....	....	....	....	....	×	....	....	....	....	....	..
alayoi	....	....	....	....	....	....	....	....	....	....	×	....	....	....	....	..
hispaniolicus	....	....	....	....	....	....	....	....	....	....	×	....	. .	....	....	..
swainsonae	....	....	....	....	....	....	....	....	....	....	....	×	....	....	....	..
kohliellus	....	....	....	....	....	....	....	....	....	×	×	×	....	....	....	..
centratus	....	....	....	....	....	....	....	....	....	....	×	....	....	....	....	?

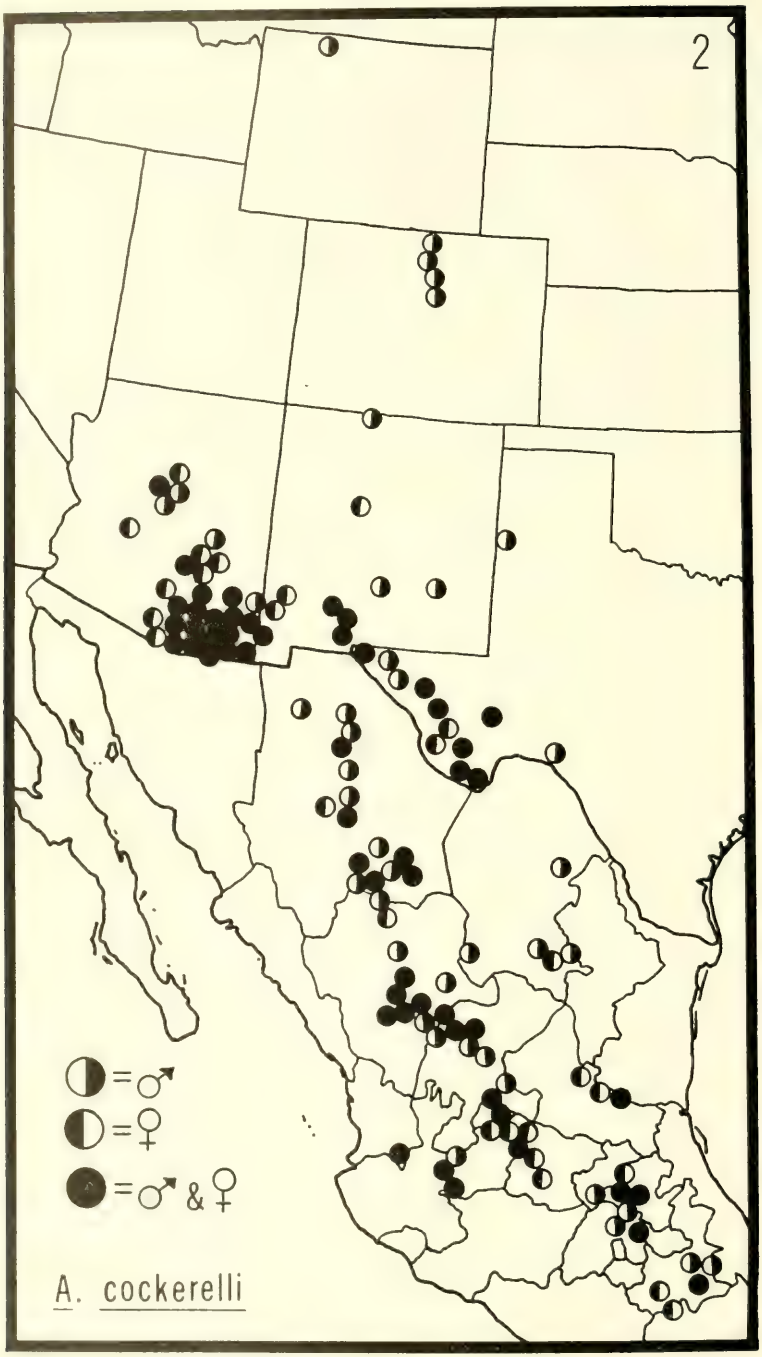


FIG. 2. Distribution of *Agapostemon cockerelli*.

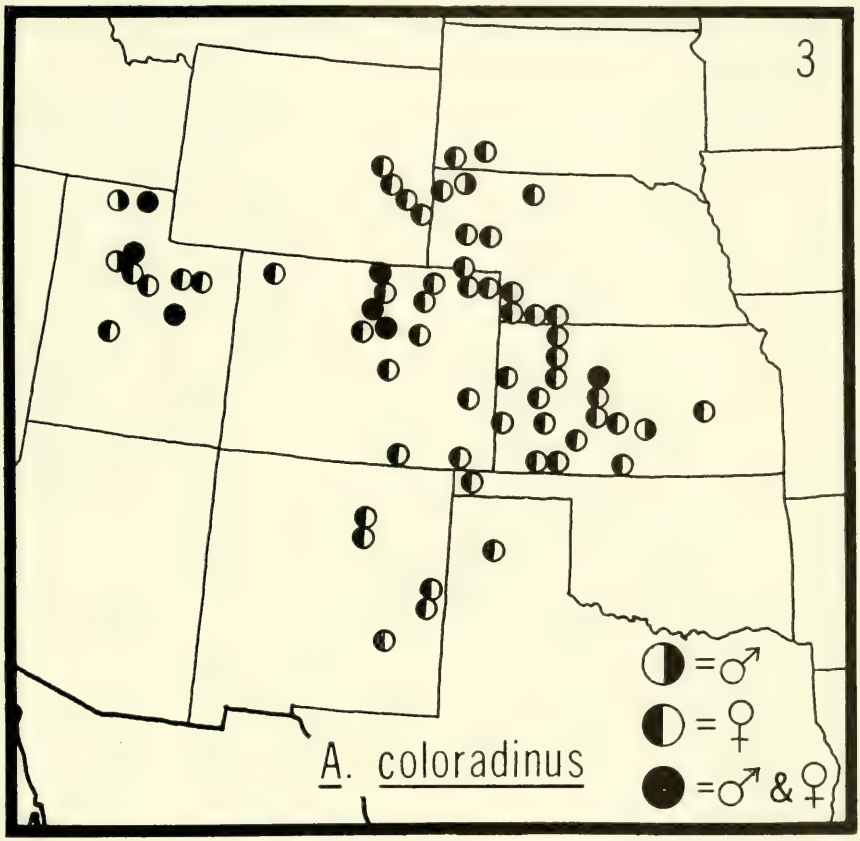


FIG. 3. Distribution of *Agapostemon coloradinus*.

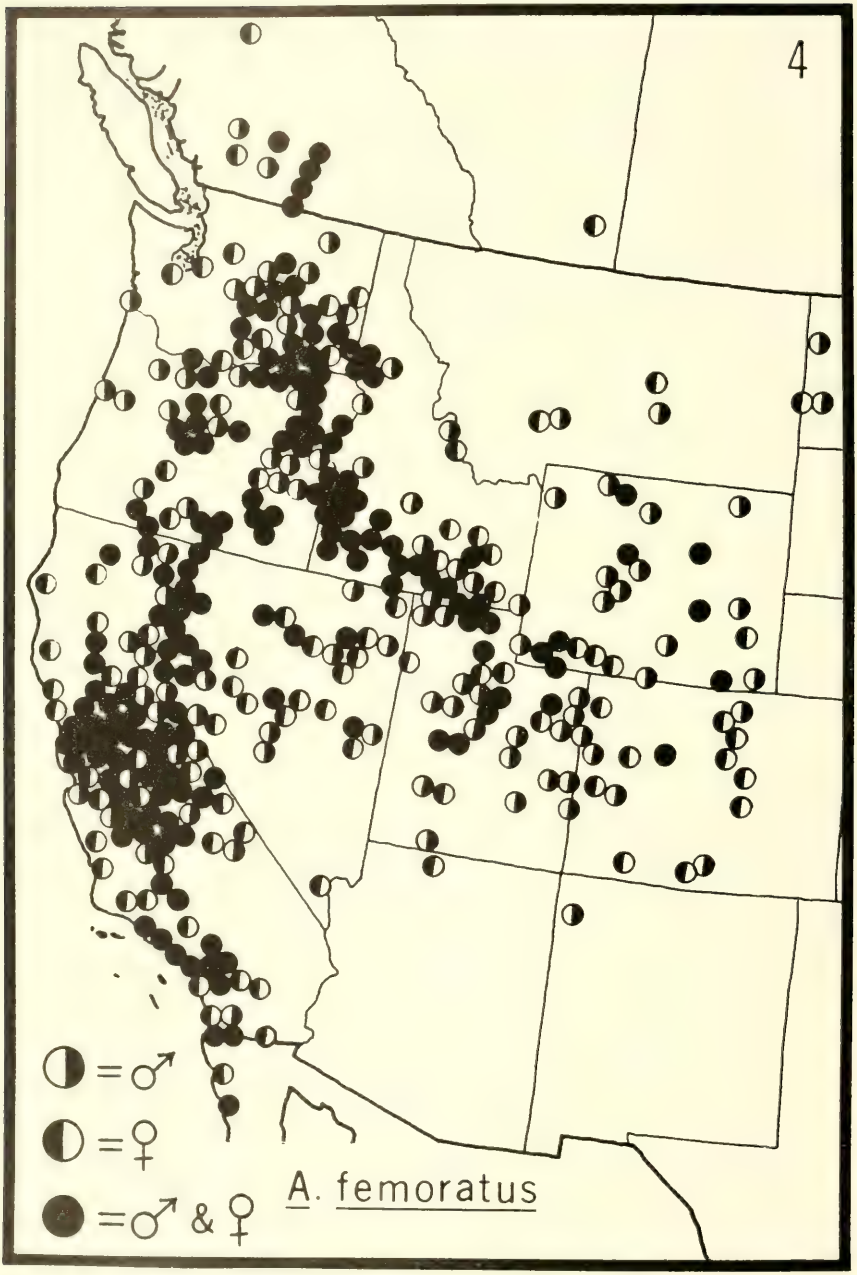


FIG. 4. Distribution of *Agapostemon femoratus*.

Fig. 5. Distribution of *Agapostemon leunculus*.

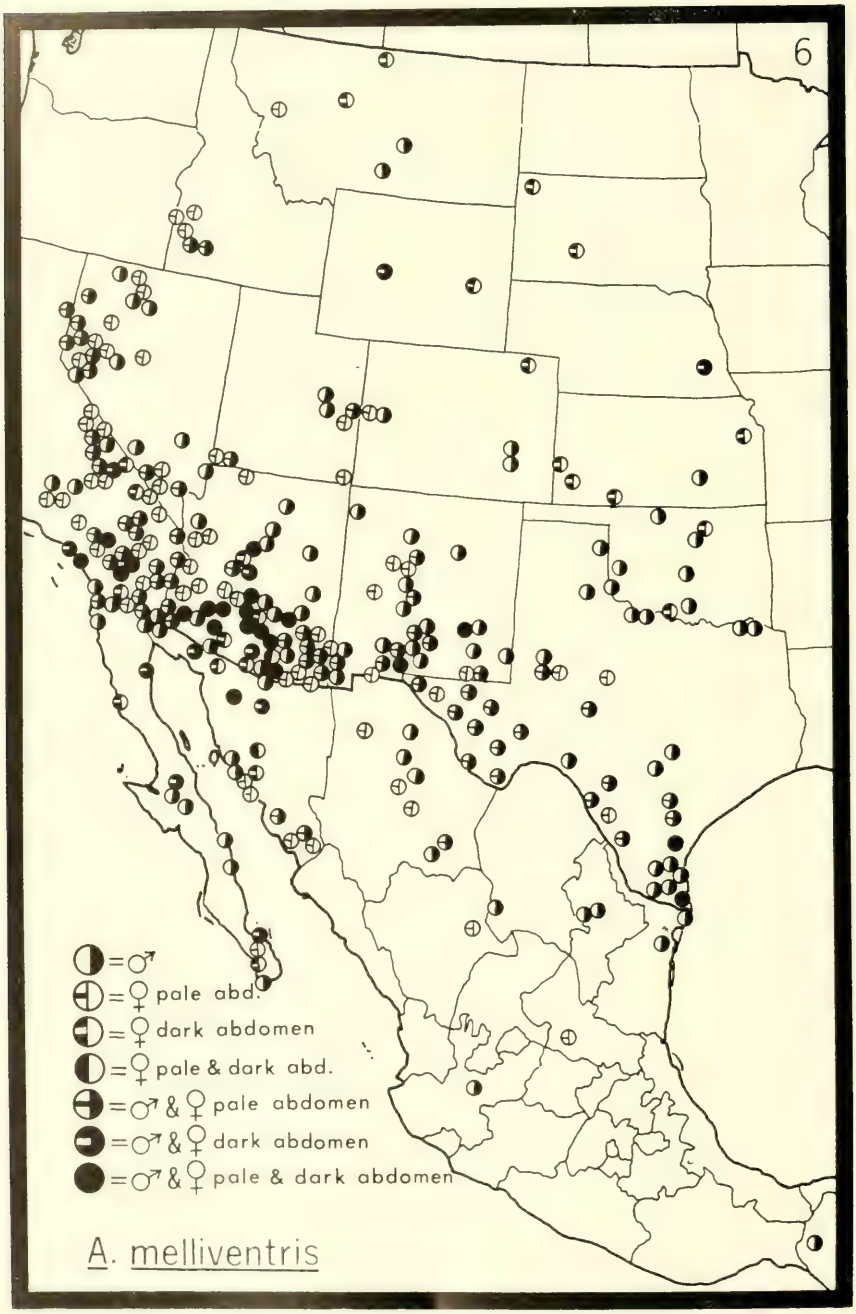


FIG. 6. Distribution of *Agapostemon melliventris*. Color of the metasomal terga of females is indicated by "dark abdomen" (= brown-black to black) and "pale abdomen" (= amber).

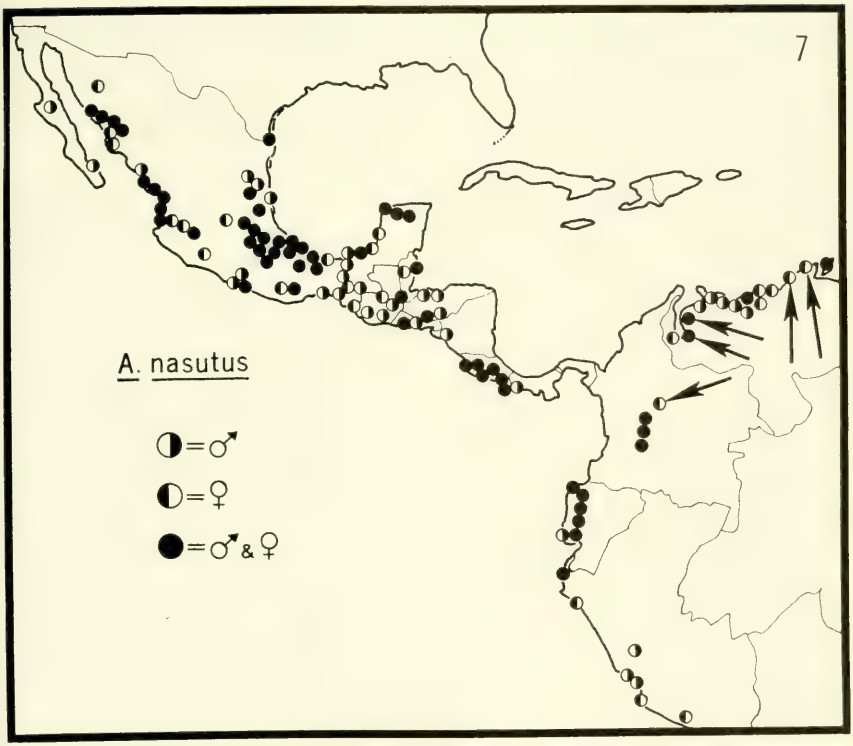
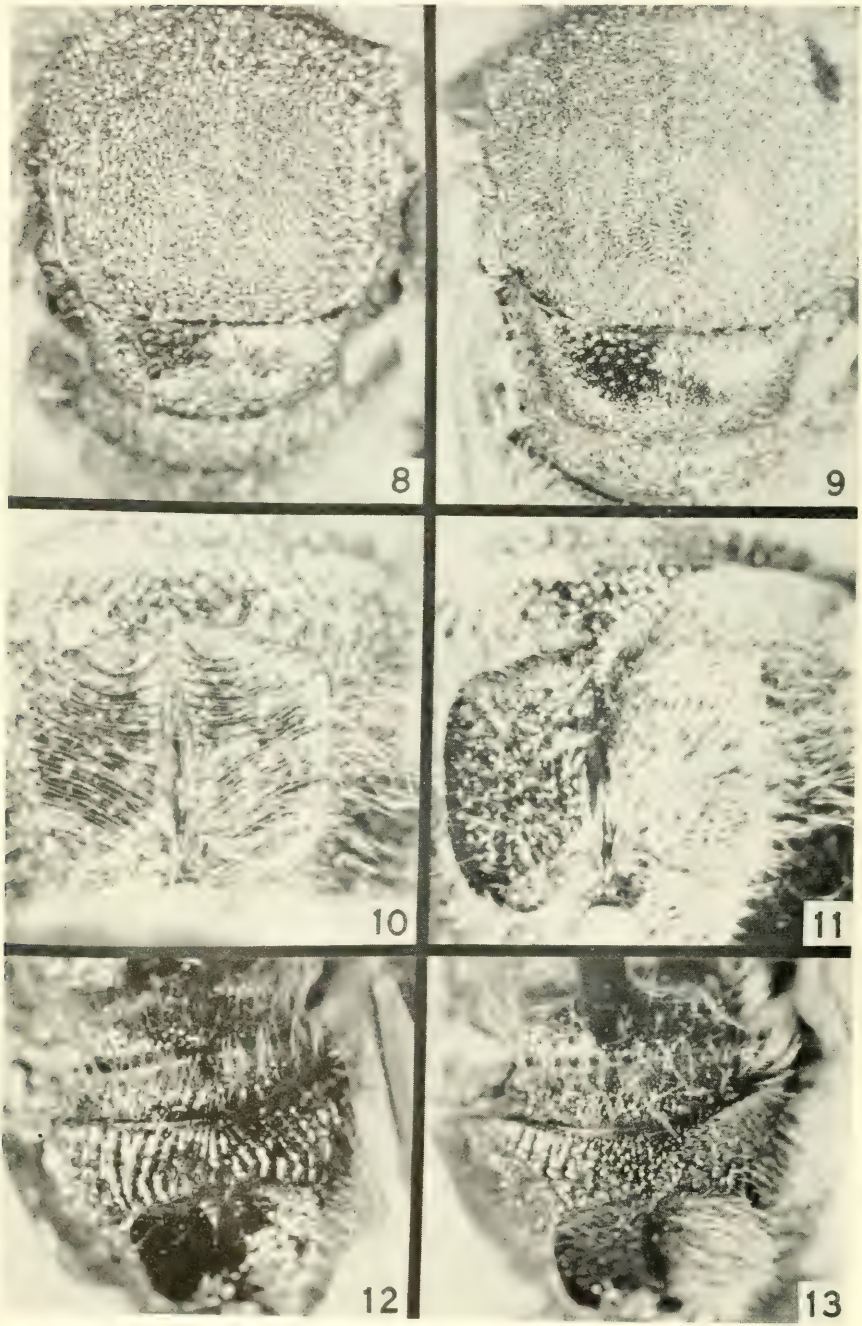
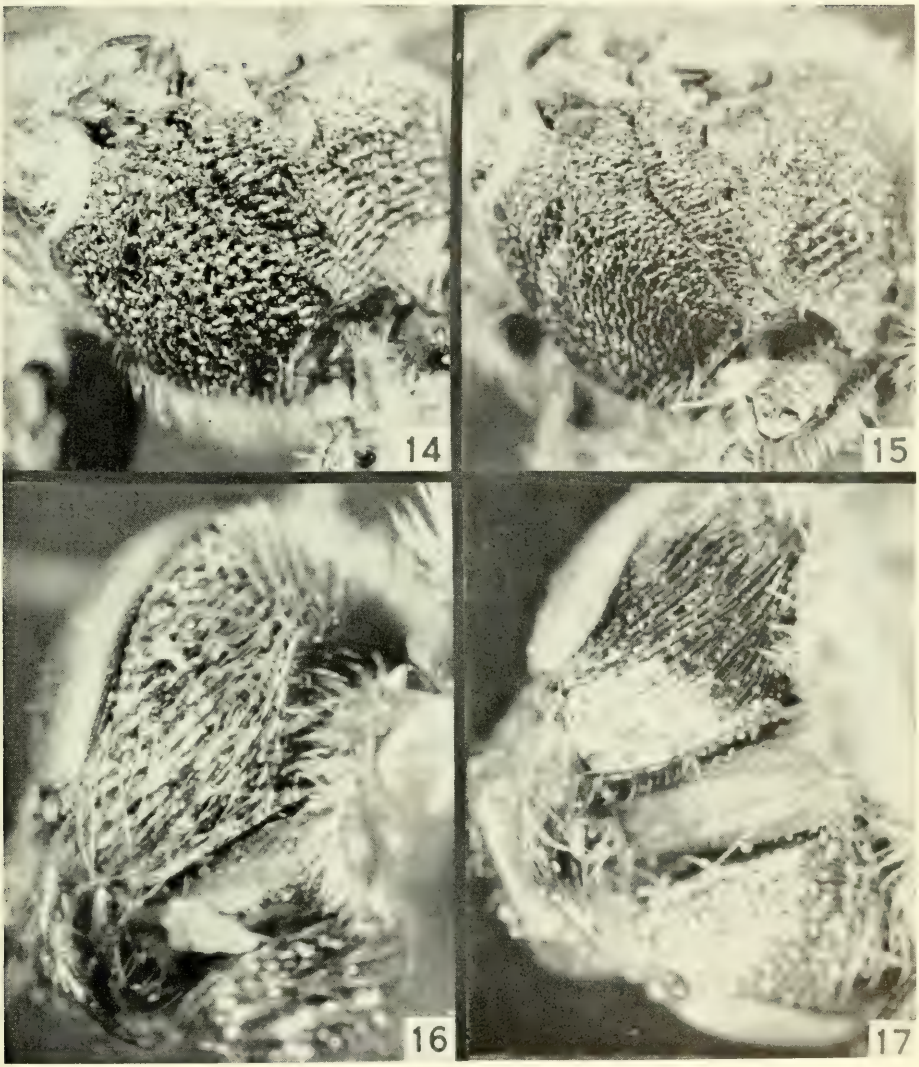


FIG. 7. Distribution of *Agapostemon nasutus* with arrows indicating localities where females with pale amber metasomal terga have been found.



FIGS. 8-13. Coarse sculpturing of *A. poeyi* (left) and finer sculpturing of *A. viequesensis* (right): **8-9,** mesonotum; **10-11,** propodeal shield; **12-13,** dorsal region of propodeum.



FIGS. **14-17.** Coarse sculpturing of *A. poeyi* (left) and finer sculpturing of *A. vicquesensis* (right): **14-15,** lateral view of mesosoma; **16-17,** ventral view of genal region.

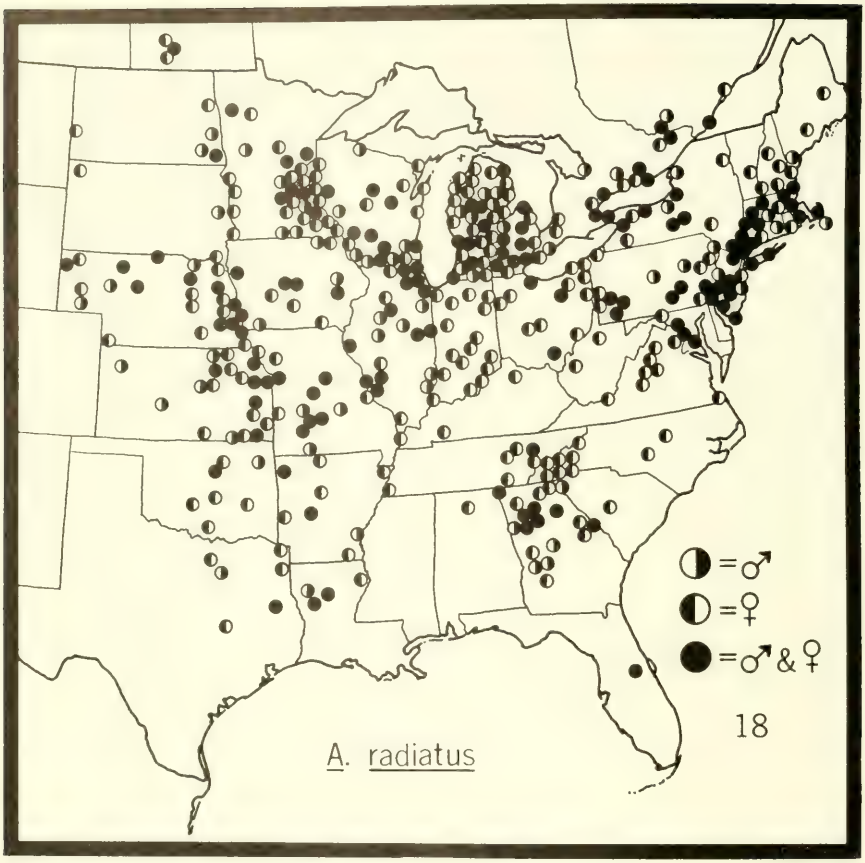


FIG. 18. Distribution of *Agapostemon radiatus*.

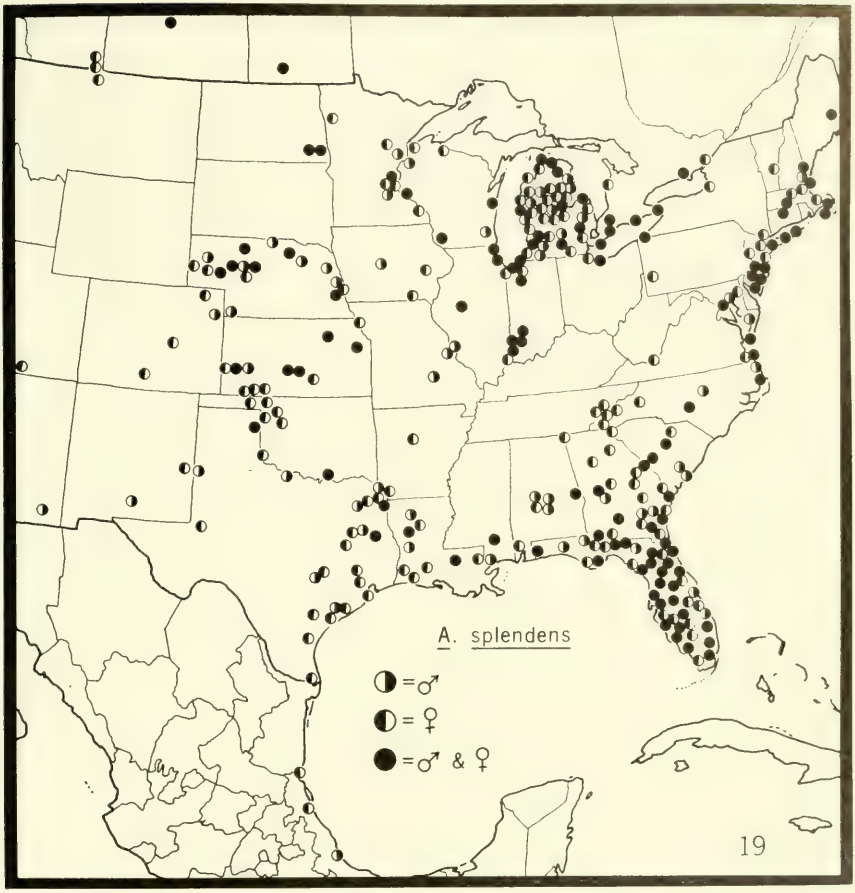


FIG. 19. Distribution of *Agapostemon splendens*.

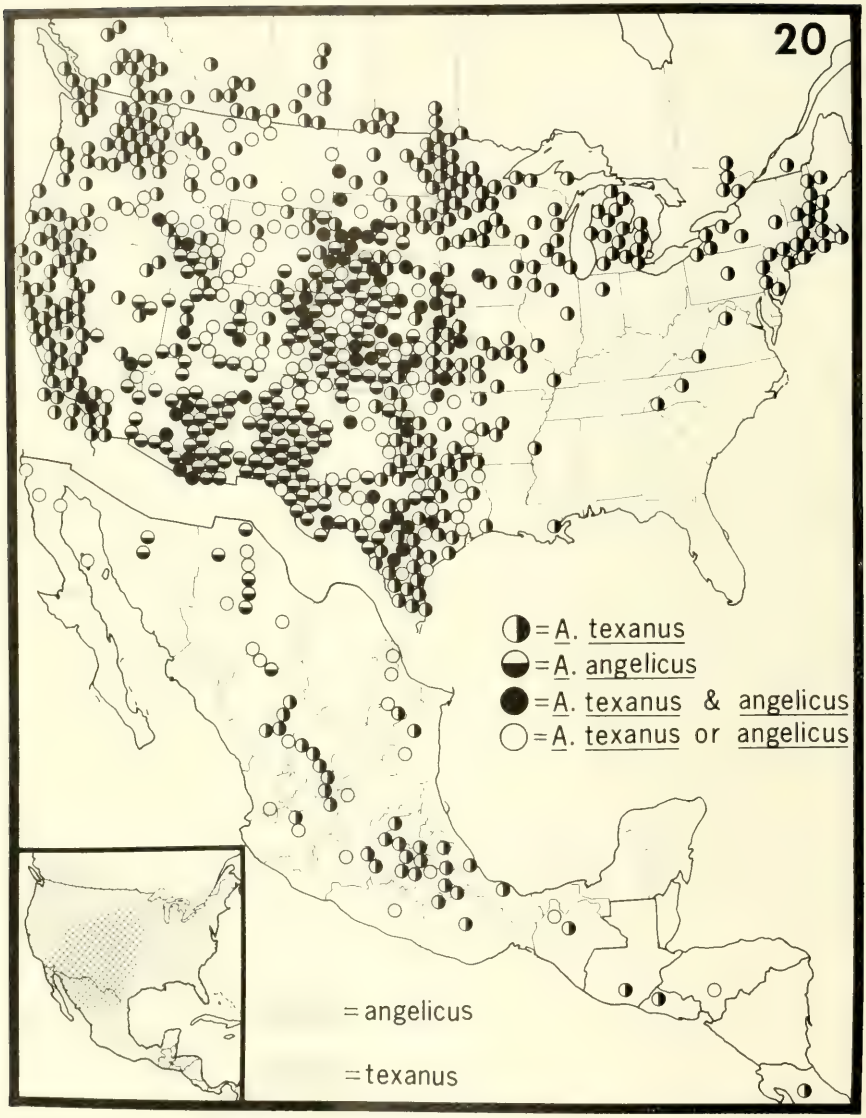
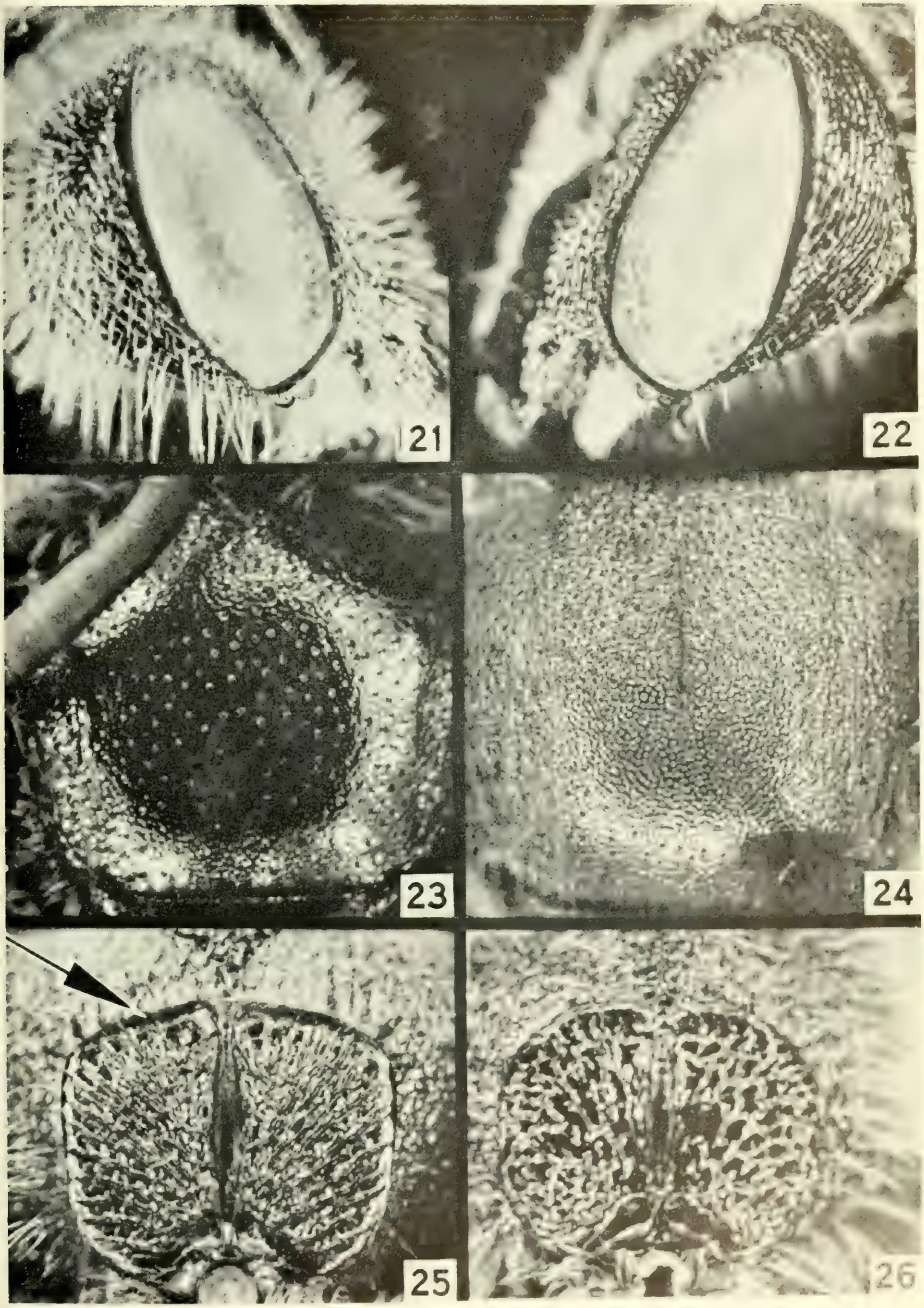


FIG. 20. Map showing distribution of *Agapostemon texanus* males and females (vertically divided circles); *Agapostemon angelicus* males only (horizontally divided circles); *A. texanus* and *A. angelicus* males (black circles); *A. texanus* and/or *A. angelicus* females (open circles).



Figs. **21-26.** *Agapostemon texanus* females: **21-22,** head with pubescence, and with pubescence removed; **23-24,** variation in mesoscutal punctation; **25-26,** variation in propodeal sculpturing. Note propodeal carina (Fig. **25,** arrow) characteristic of female *Agapostemon*.

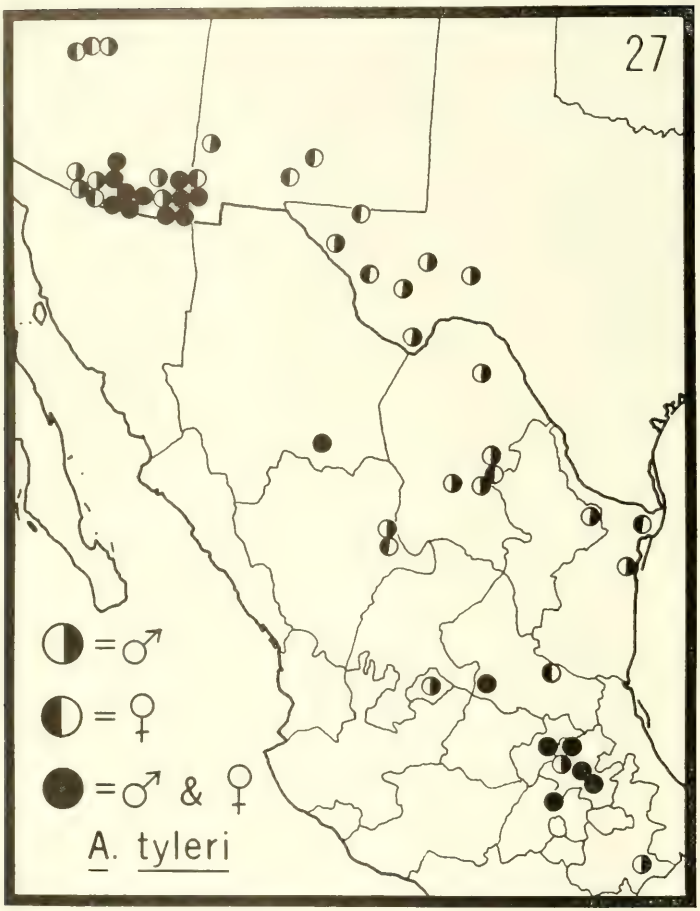
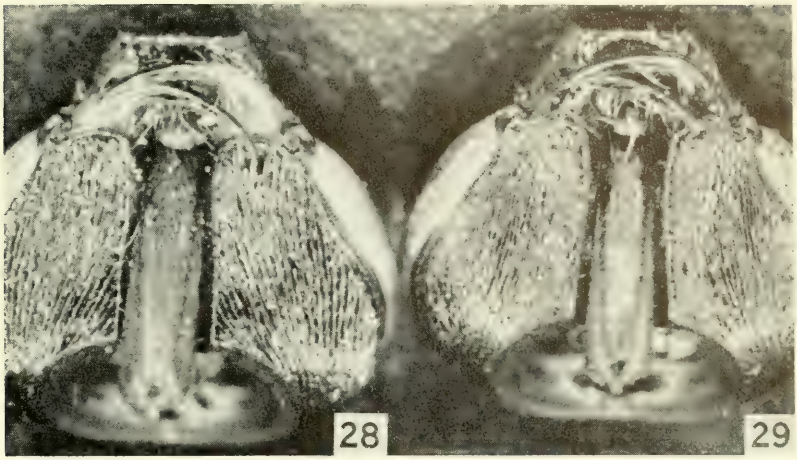


FIG. 27. Distribution of *Agapostemon tyleri.*



FIGS. 28-29. Ventral view of genal region of *Agapostemon virescens* (left) and *A. tyleri* (right).

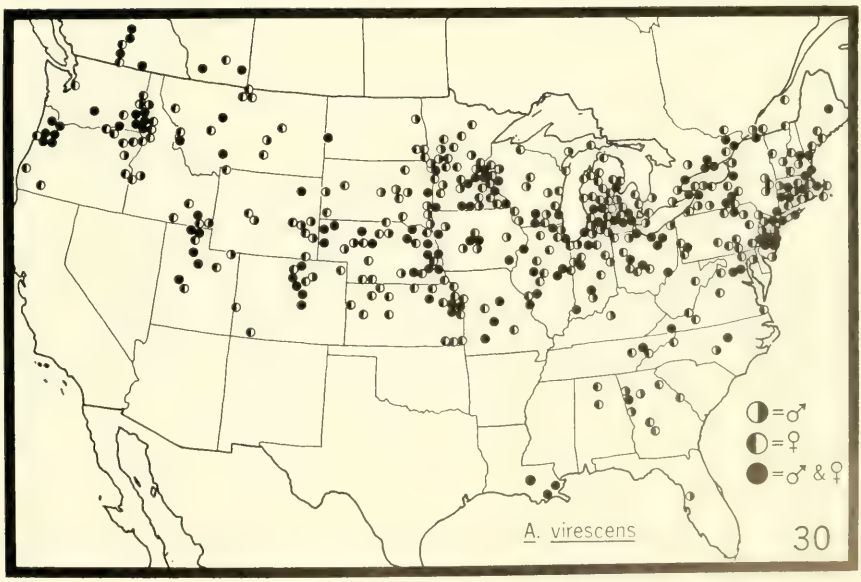
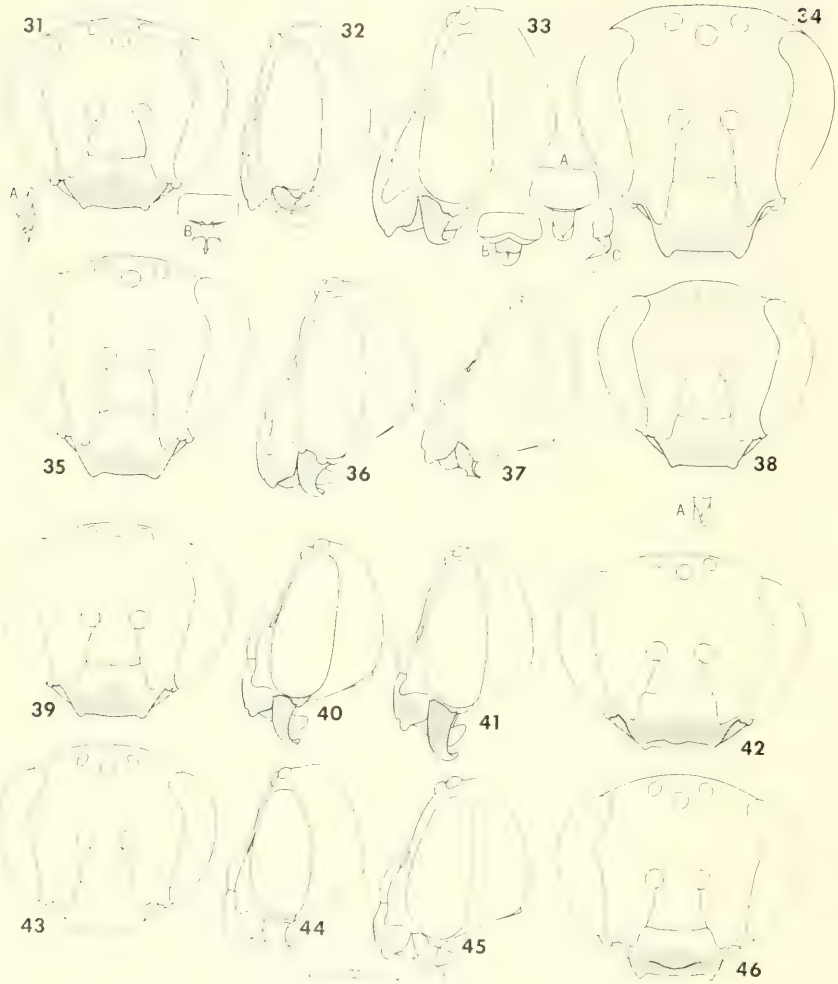
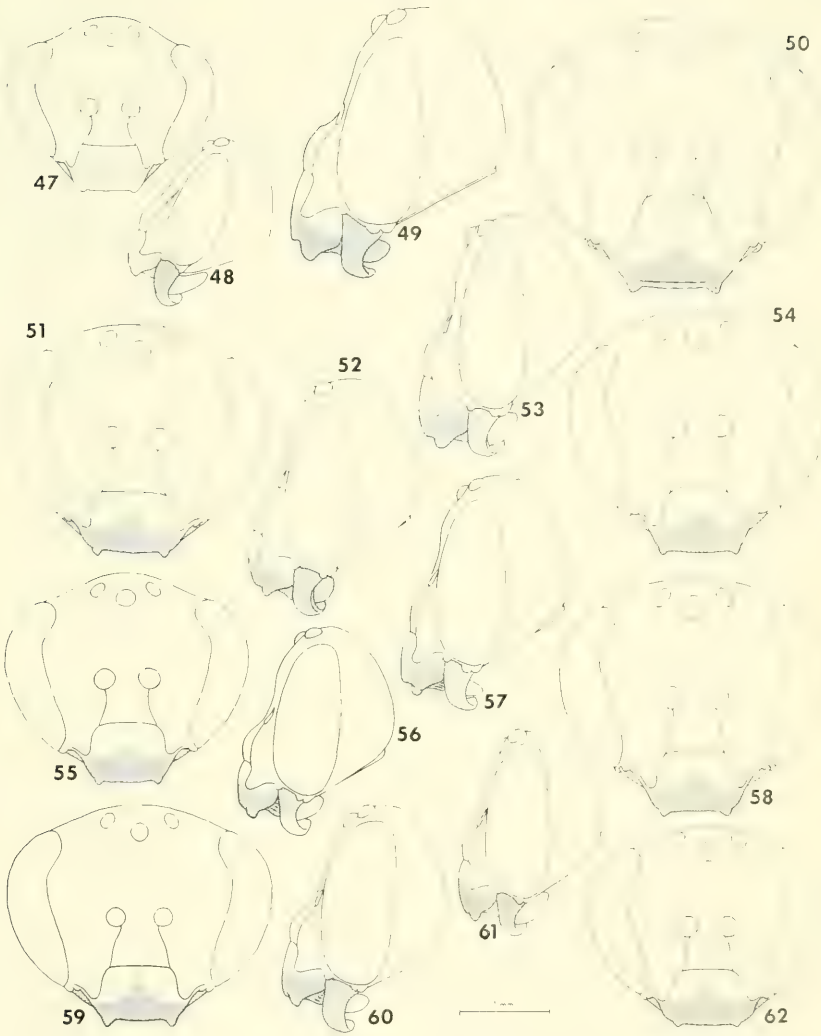


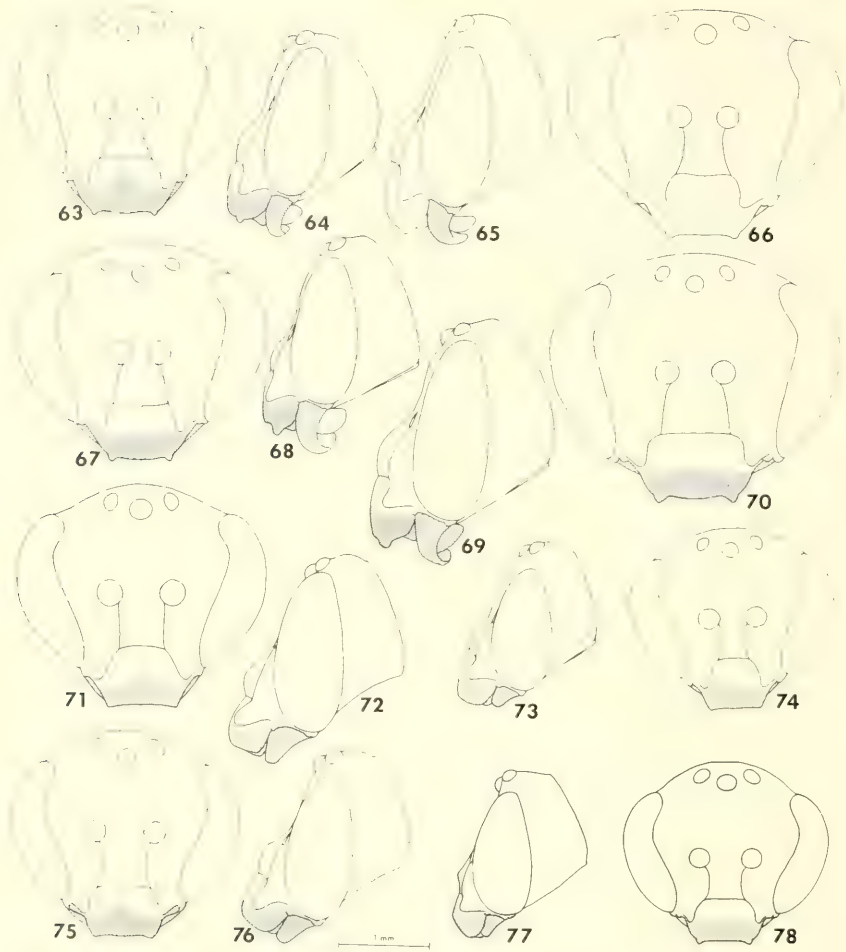
FIG. 30. Distribution of *Agapostemon virescens*.



FIGS. **31-46.** Heads of female *Agapostemon* in anterior and lateral views: **31-32,** *A. kohliellus* (stippling yellow) with lateral (A) and anterior (B) views of labrum; **33-34,** *A. viridulus* (stippling brown) with anterior (A), antero-distal (B) and lateral (C) views of labrum; **35-36,** *A. swainsonae* (stippling amber); **37-38,** *A. hispaniolicus* (stippling brown) with anterior view (A) of apex of labrum; **39-40,** *A. viequesensis* (stippling brown); **41-42,** *A. nasutus* (stippling yellow); **43-44,** *A. atrocaeruleus;* **45-46,** *A. leunculus* (stippling yellow).

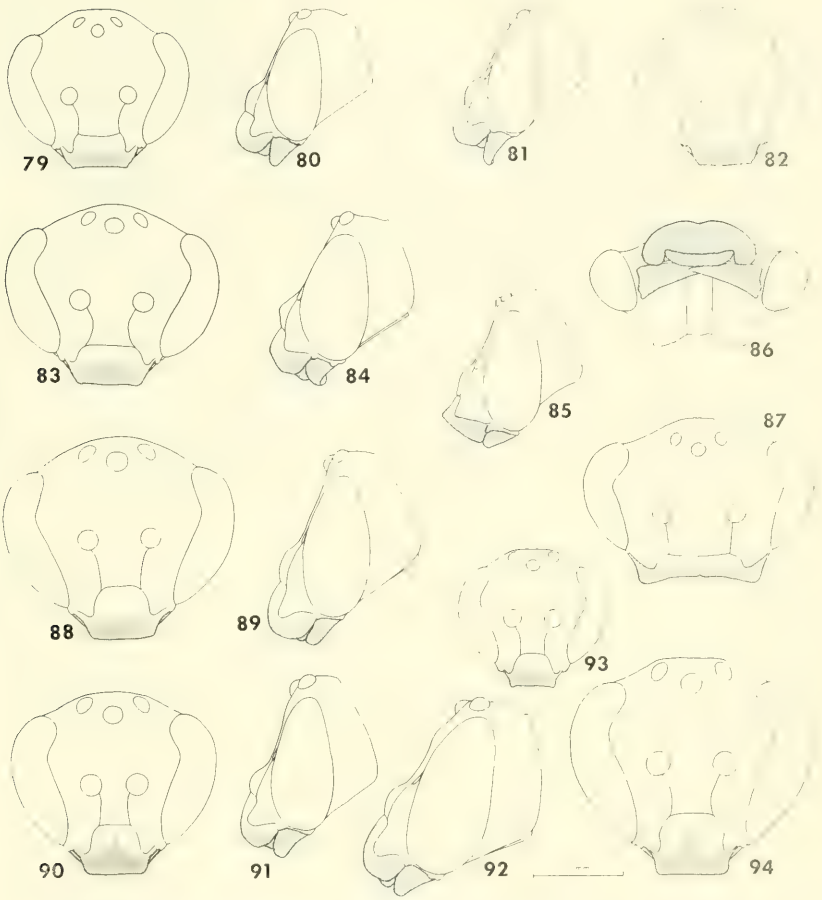


FIGS. **47-62.** Heads of female *Agapostemon* in anterior and lateral views: **47-48,** *A. intermedius* (stippling yellow); **49-50,** *A. coloradinus* (stippling brown-black); **51-52,** *A. tyleri* (stippling brown-black); **53-54,** *A. virescens* (stippling brown-black, hatching yellow); **55-56,** *A. radiatus* (stippling black, hatching yellow); **57-58,** *A. femoratus* (stippling black, hatching orange); **59-60,** *A. cockerelli* (stippling black, hatching yellow); **61-62,** *A. melliventris* (stippling yellow).

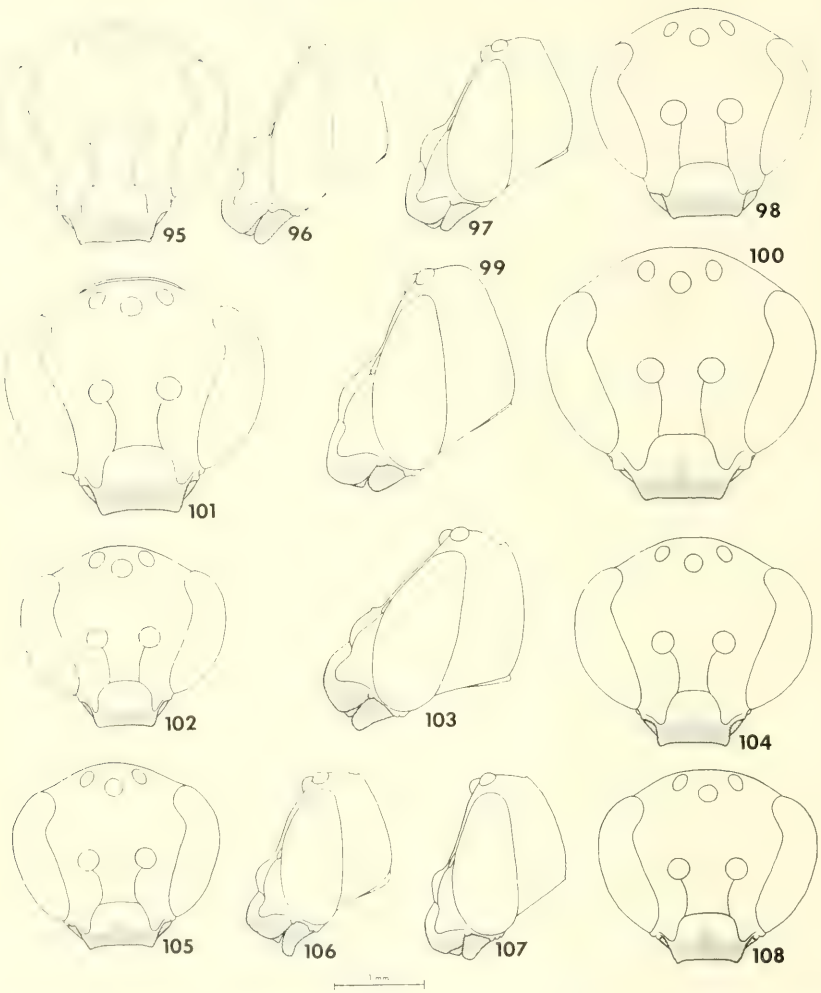


FIGS. **63-70.** Heads of female *Agapostemon* in anterior and lateral views: **63-64,** *A. mexicanus* (stippling amber, hatching yellow); **65-66,** *A. peninsularis* (stippling yellow); **67-68,** *A. texanus* or *A. angelicus* (stippling black, hatching yellow); **69-70,** *A. splendens* (stippling brown-black, hatching amber).

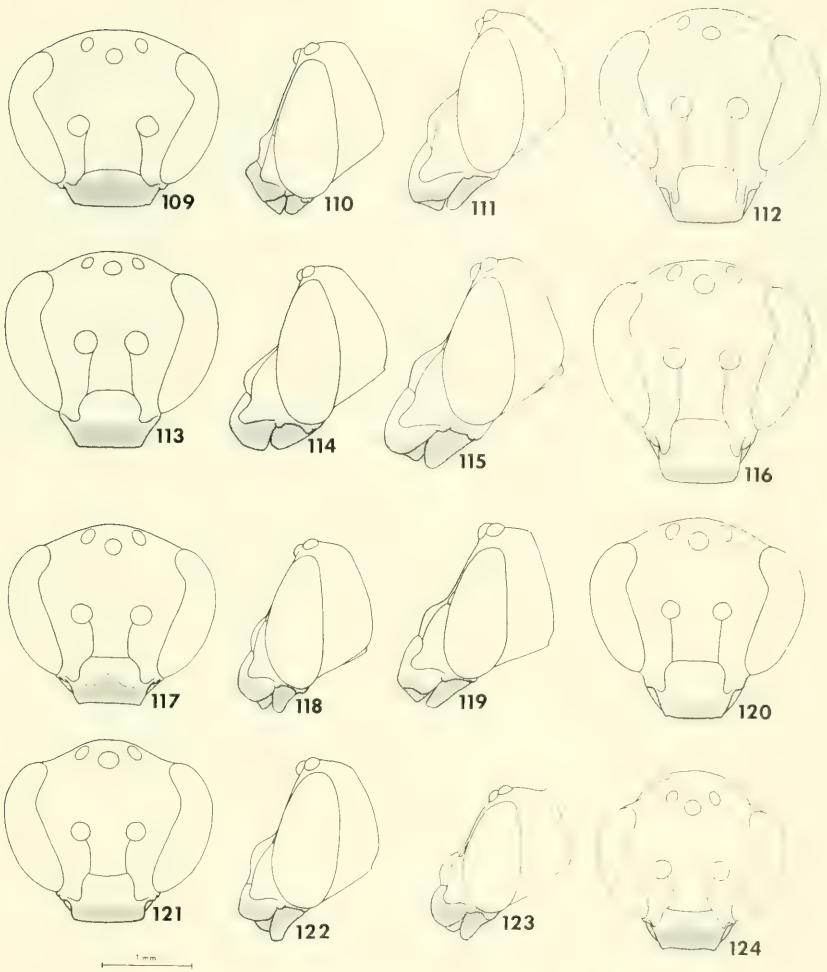
FIGS. **71-78.** Heads of male *Agapostemon* in anterior and lateral views (stippling yellow): **71-72,** *A. splendens;* **73-74,** *A. angelicus;* **75-76,** *A. texanus;* **77-78,** *A. rhopalocera.*



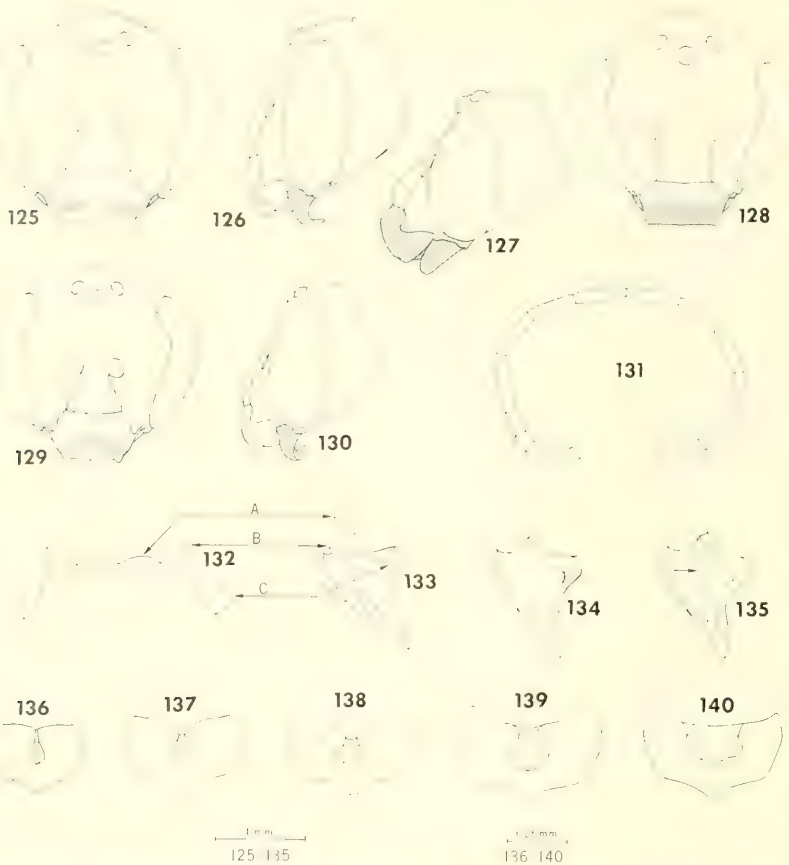
Figs. **79-94.** Heads of male *Agapostemon* in anterior and lateral views (Fig. **86,** ventral view): **79-80,** *A. atrocaeruleus;* **81-82,** *A. intermedius;* **83-84,** *A. leunculus;* **85-87,** *A. nasutus;* **88-89,** *A. peninsularis;* **90-91,** *A. mexicanus;* **92-94,** *A. melliventris* (note size variation of two specimens, **93-94,** collected at the same time and place). Yellow or creamy maculations are indicated with stippling.



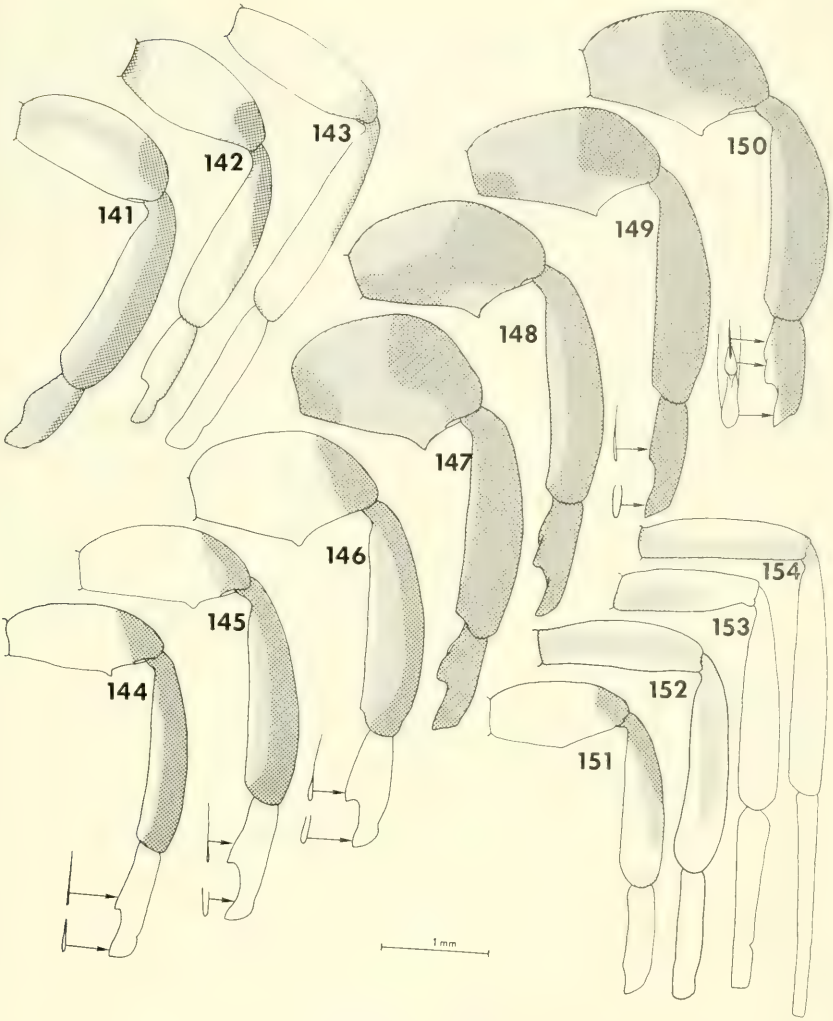
FIGS. 95-108. Heads of male *Agapostemon* in anterior and lateral views: **95-96,** *A. tyleri;* 97-98, *A. virescens;* 99-100, *A. coloradinus;* 101-104, *A. femoratus* (note size variation, 101-102); 105-106, *A. radiatus;* 107-108, *A. cockerelli.* Yellow or creamy maculations are indicated with stippling.



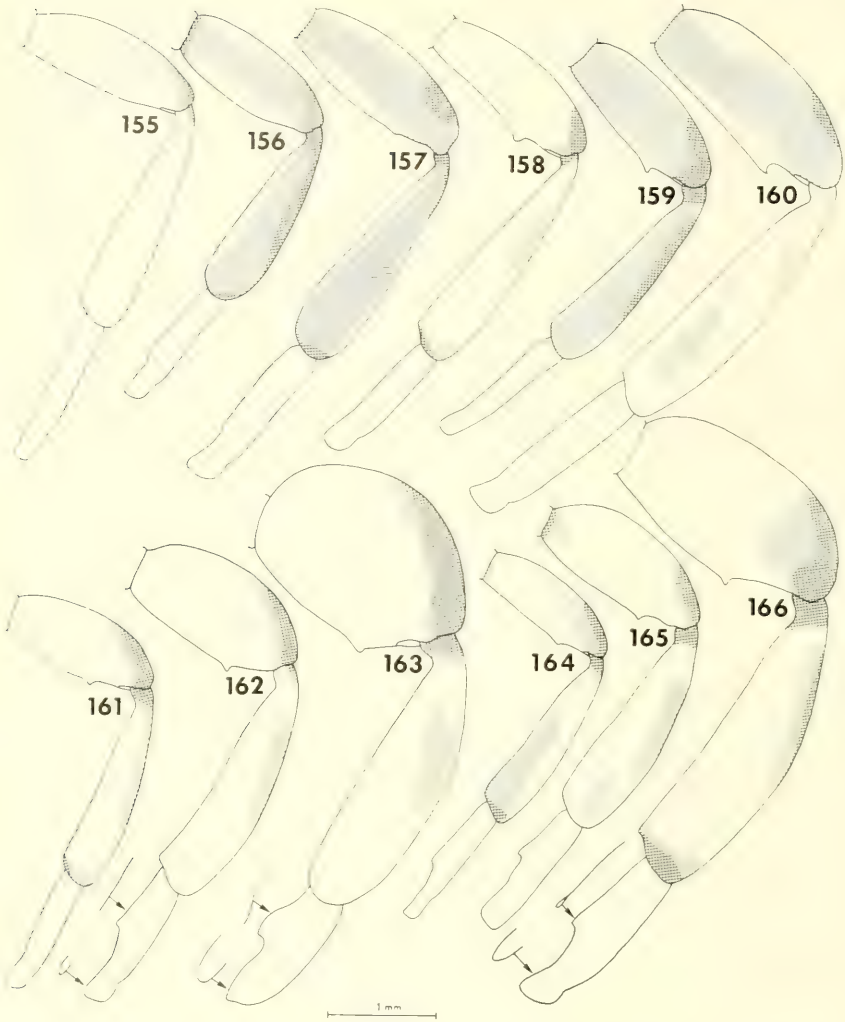
FIGS. **109-124.** Heads of male *Agapostemon* in anterior and lateral views: **109-110,** *A. kohliellus;* **111-112,** *A. viridulus,* **113-114,** *A. swainsonae;* **115-116,** *A. hispaniolicus;* **117-118,** *A. viequesensis;* **119-120,** *A. cubensis;* **121-122,** *A. centratus;* **123-124,** *A. semimelleus.* Yellow or creamy maculations are indicated with stippling.



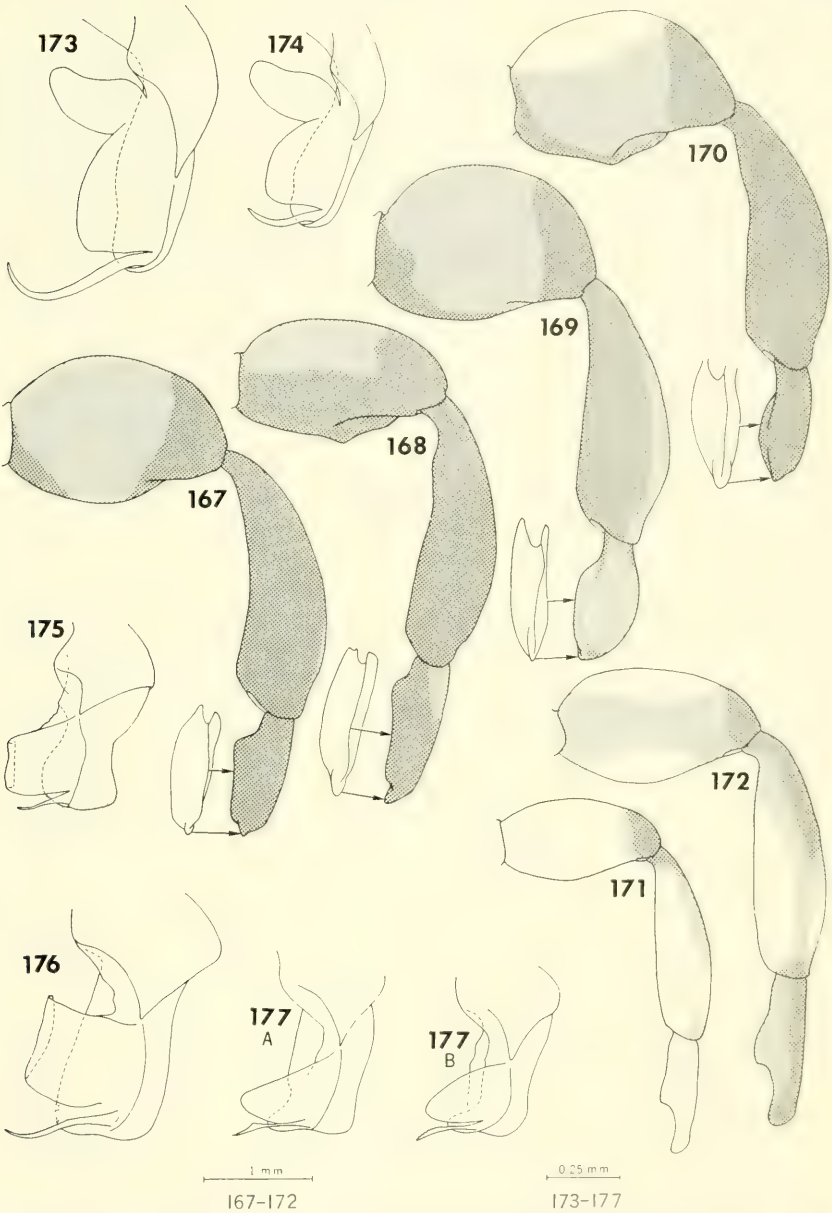
FIGS. 125-140. **125-130,** heads of *Agapostemon* in anterior and lateral views, with yellow maculations stippled: **125-126,** *A. mourei* female; **127-128,** *A. mourei* male; **129-130,** *A. semimelleus* female; **131,** dorsal view of *A. rhopalocera* male right antenna; **132-133,** dorsal and lateral views of male *A. mourei* pronotum showing overlapping mesoscutum (A), acute lateral angle (B), and angular posterior lobe (C); **134,** lateral view of female *A. nasutus* pronotum showing yellow maculation (stippling); **135,** lateral view of female *A. leunculus* pronotum showing carina (arrow) not found on *A. nasutus;* **136-140,** last visible (6th) male sternites: **136,** *A. intermedius;* **137,** *A. boliviensis;* **138,** *A. lanosus;* **139,** *A. mourei;* **140,** *A. inca.*



FIGS. **141-154.** Anterior views of male *Agapostemon* hind femur, tibia and basitarsus. Color yellow or creamy with brown or black maculations. Anterior maculations with left oblique or vertical hatching; posterior maculations with right oblique or horizontal hatching; anterior and posterior maculations with cross hatching. **141,** *A. kohliellus;* **142,** *A. atrocaeruleus:* **143,** *A. leunculus;* **144,** *A. poeyi;* **145,** *A. viequesensis;* **146,** *A. jamaicensis;* **147,** *A. swainsonae:* **148,** *A. hispaniolicus;* **149,** *A. cubensis;* **150,** *A. viridulus;* **151,** *A. intermedius;* **152,** *A. centratus;* **153,** *A. nasutus;* **154,** *A. rhopalocera.* Arrows indicate ventral views of basal ridge and apical groove on basitarsus.

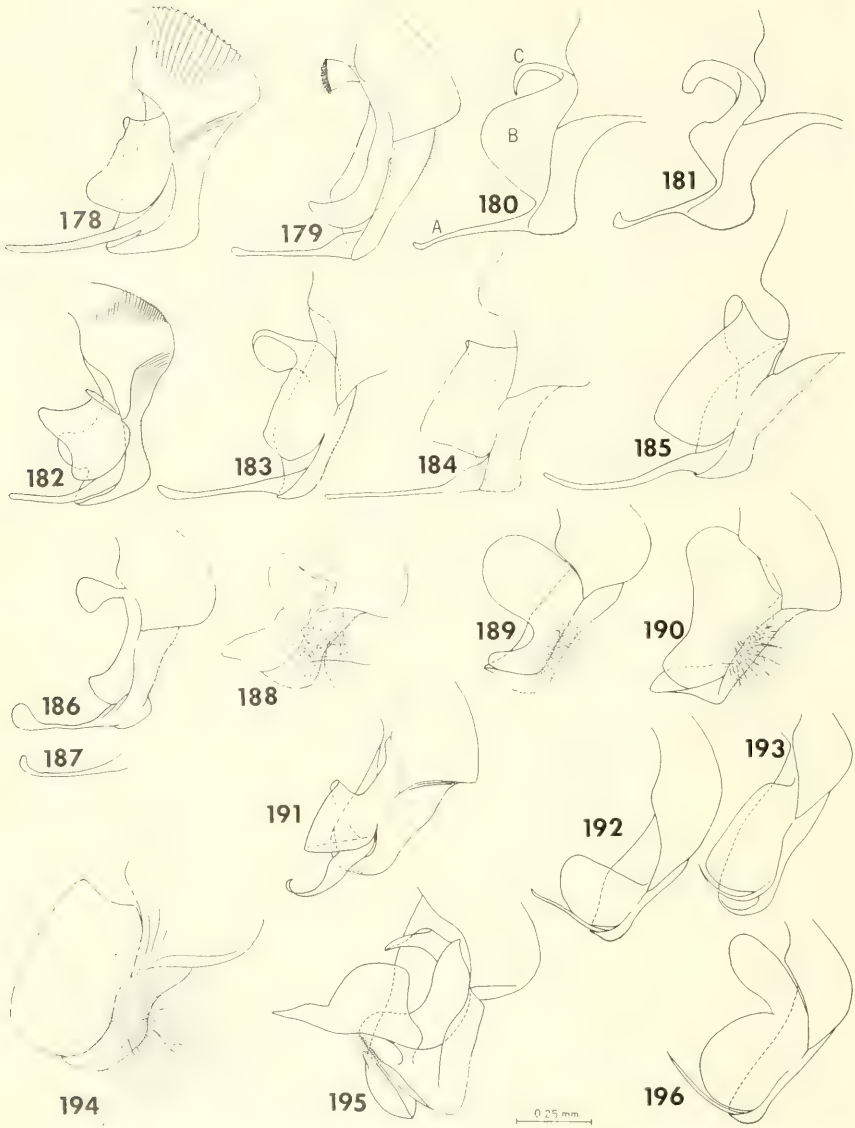


FIGS. **155-166.** Anterior views of male *Agapostemon* hind femur, tibia, basitarsus. Color yellow or creamy with brown or black maculations. Anterior maculations with vertical hatching; posterior maculations with horizontal hatching; anterior and posterior maculations with cross hatching. **155,** *A. melliventris;* **156,** *A. mexicanus;* **157,** *A. peninsularis;* **158,** *A. virescens;* **159,** *A. tyleri;* **160,** *A. coloradinus;* **161,** *A. radiatus;* **162,** *A. cockerelli;* **163,** *A. femoratus;* **164,** *A. angelicus;* **165,** *A. texanus;* **166,** *A. splendens.* Arrows indicate ventral views of basal ridge and apical groove on basitarsus.

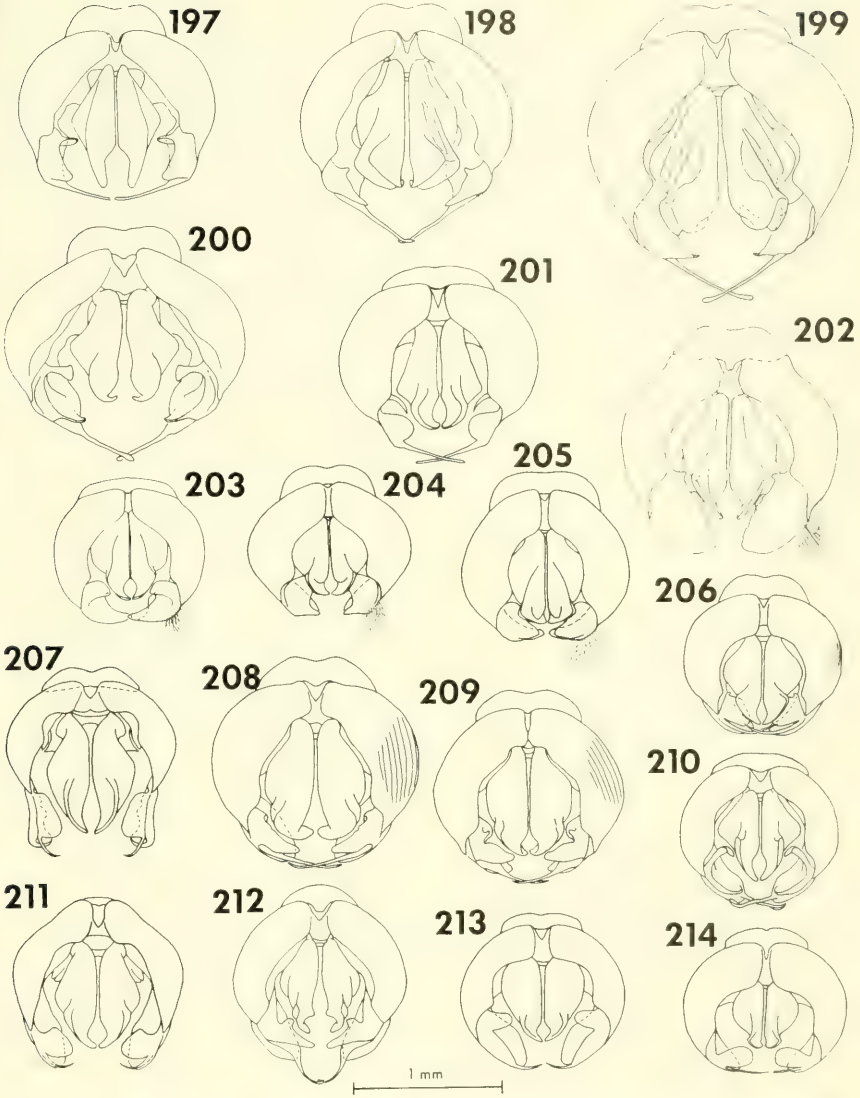


FIGS. **167-172.** Anterior views of male *Agapostemon* hind femur, tibia, basitarsus. Color yellow or creamy with brown or black maculations. Anterior maculations with left oblique hatching; posterior maculations with right oblique hatching; anterior and posterior maculations with cross hatching. **167,** *A. mourei;* **168,** *A. inca;* **169,** *A. lanosus;* **170,** *A. boliviensis;* **171,** *A. semimelleus;* **172,** *A. chapadensis.* Arrows indicate ventral views of basal ridge and apical groove on basitarsus.

FIGS. **173-177.** Apical view of male gonostyli (right side): **173,** *A. chapadensis;* **174,** *A. semimelleus;* **175,** *A. inca;* **176,** *A. mourei;* **177A,** *A. boliviensis;* **177B,** *A. lanosus.*



FIGS. 178-196. Apical view of male gonostyli (right side): **178,** *Agapostemon viridulus;* **179,** *A. splendens;* **180,** *A. texanus* (A, apical stylus; B, medial plate; C, basal stylus); **181,** *A. angelicus;* **182,** *A. centratus;* **183,** *A. virescens;* **184,** *A. tyleri;* **185,** *A. coloradinus;* **186,** *A. poeyi;* **187,** *A. viequesensis;* **188,** *A. melliventris;* **189,** *A. mexicanus;* **190,** *A. peninsularis;* **191,** *A. kohliellus;* **192,** *A. intermedius;* **193,** *A. leunculus;* **194,** *A. femoratus;* **195,** *A. nasutus;* **196,** *A. atrocaeruleus.*



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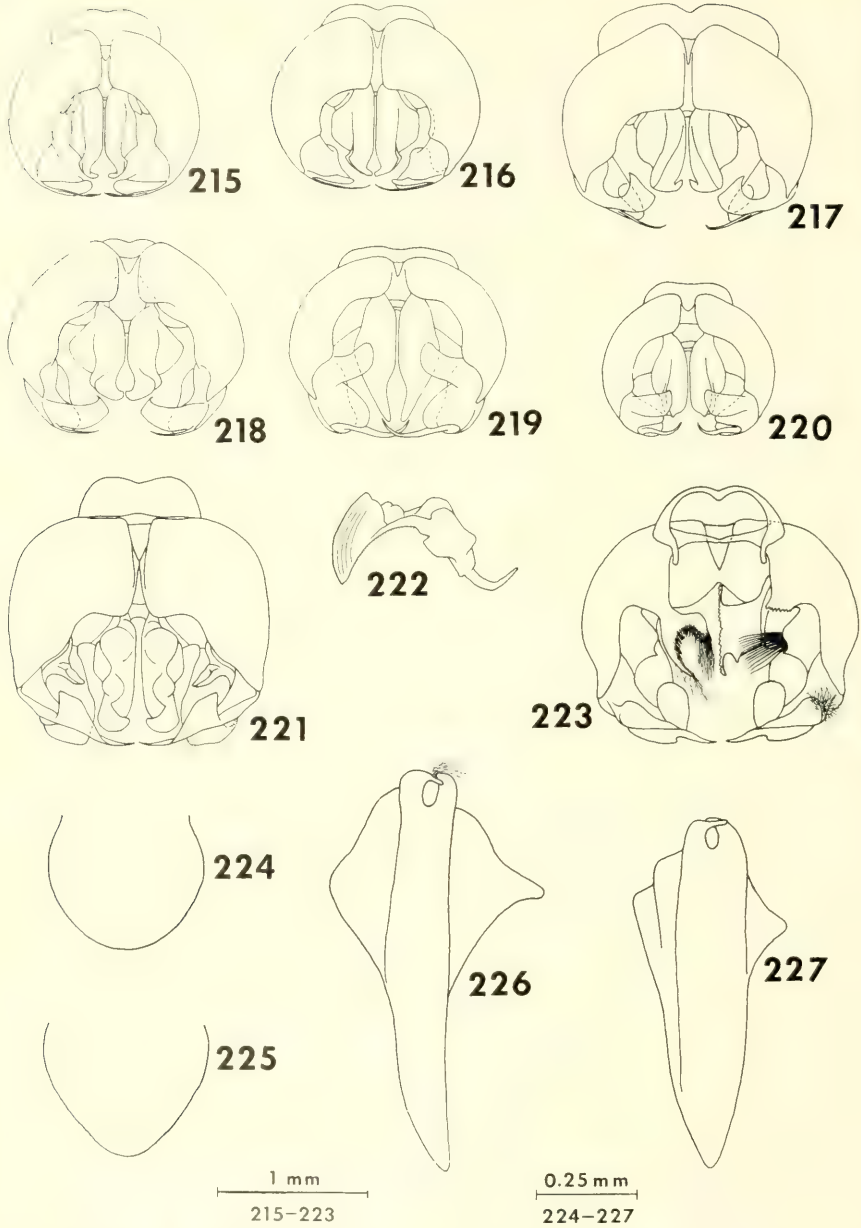

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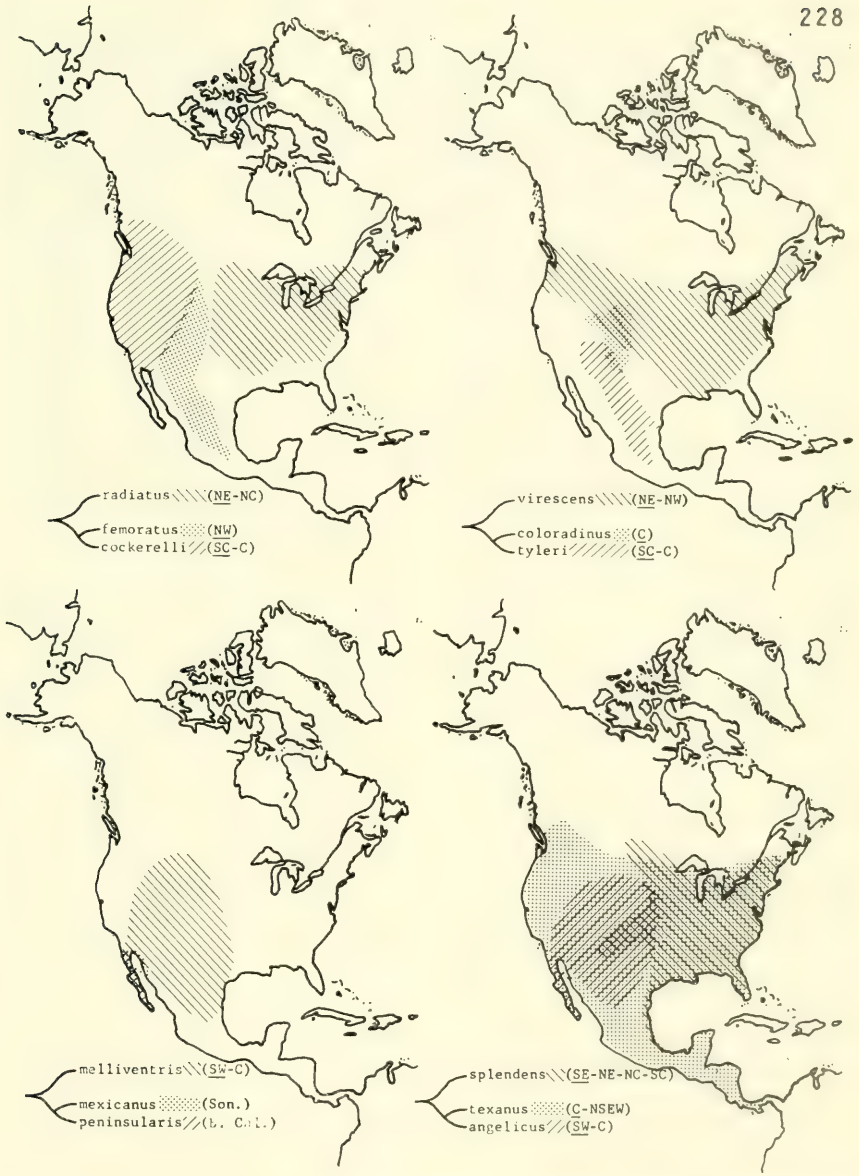

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Comparative Morphological and Histochemical Studies of Stomachs of Selected American Bats

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ABSTRACT

Stomachs of 13 species of North American bats representing genera of six families and several different types of feeding habits were examined and compared morphologically, histologically, and histochemically. All species studied were found to have morphologically distinct stomachs; relationships between gastric structure and physiology, and between gastric structure and consumption of particulate food materials were investigated. Four histochemical procedures were employed to examine qualitative and quantitative features of mucins in the gastric mucosa and the glands of Brunner. Stomachs of insectivorous and carnivorous bats studied generally were of simpler structure than the more specialized stomachs of frugivorous and sangivorous kinds, with various degrees of intermediacy in structure noted in two more or less omnivorous species. Results of histochemical studies indicate greatest overall production of mucus in insectivorous and carnivorous bats.

Some systematic relationships among families, subfamilies, and genera are discussed in light of results of gastric studies. Apparent coevolution of gastric morphology with a progressive change from albuminous to cellular feeding within the family Phyllostomatidae also is discussed.

INTRODUCTION

Definitive phylogenetic studies of bats have been hampered by lack of an adequate fossil record for this group. The earlier-supposed relationships (Dobson, 1875; Miller, 1907) of major taxa in the Chiroptera have been questioned in recent years, leading to a search for, and subsequent use of, a whole suite of approaches and characteristics not heretofor employed in the classification of these mammals. The purpose of this study was to examine the structure of the gastric portion of the intestinal tract for possible use as a criterion in studying relationships among bats. Additionally, because mammalogists and mammalian paleontologists have long used selected structures of the teeth, palate, and masticatory musculature in examining coevolution of morphology and food habits in various groups of mammals, this study also attempts to correlate gastric morphology with food habits.

The objectives of the present study were fourfold. The first aim was to increase our knowledge of the gastric structure of bats along with detailed comparisons of the gastric mucosae. Second, some histochemical properties

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of the gastric and duodenal mucins were examined and described. Third, the results of the above investigations were evaluated with respect to diverse and usually obligate feeding habits of various bat species, in an attempt to demonstrate the presence or absence of coevolution in feeding preferences and gastric structure. Lastly, gastric morphology and distribution of various mucosubstances (as revealed by selected histochemical procedures) were considered in the light of the presently recognized phylogenetic arrangement of the species under examination.

Published comparative studies of mammalian soft anatomy are, for the most part, inadequate, because the variability among species is rather poorly documented. Deficiencies are especially apparent for the post-lingual portions of the gastrointestinal tract of mammals. With the exception of a few accounts dealing with domesticated animals and various groups of rodents and insectivores, most comparative anatomical studies of stomachs make reference to only a few species, or concern specific physiological problems in specific species. Such studies have left gaps in our knowledge of how much stomachs of relatively closely related taxa differ structurally and physiologically. Also, because there are few comparative studies of the gastric mucosal membrane, relatively little has been suggested regarding the relationship of gastric structure to feeding habits, other than a few well-entrenched generalizations about certain domesticated mammals. This paper presents new information regarding the coevolution of food habits with gastric structure in bats.

According to Cuvier (1805), there were three distinguishable forms that could be recognized; the transversely elongated tubular stomach possessed by bats that eat fruit, the globular stomach with closely approximated cardiac and pyloric orifices exhibited by insectivorous bats, and the elongated "conical" stomach, with a specialized pyloric caecum, of blood feeders. The last of these categories is immediately questionable because of the fact that the species upon which the category is based were probably not blood-feeding species, but nectar- or fruit-eaters. Huxley (1865), subsequent to reviewing Cuvier's classification, described the stomach of the truly blood-feeding vampire bat (*Desmodus*), in which he found the cardiac portion to be a tremendously elongated caecum, the cardiac and pyloric orifices close together, and the region of the pyloric mucosa notably abbreviated. Owen (1868) gave his own interpretation of various types of stomachs of bats in relation to diet, including one poorly defined category concerning "times of taking the food and to the quantity taken."

The important work of Robin (1881) represents the first detailed published comparative account of gastrointestinal structure in bats. Robin's paper includes an excellent review of earlier work, along with new information that led him to discard the classifications of Cuvier and Owen as

inconsistent with his own observations. Robin noted three shapes of stomachs as demonstrated by the 1) Megachiroptera (Pteropodidae), 2) Microchiroptera (*Nyctimene*) and 3) *Desmodus* (distinctive type of vampire bats). He also discussed variation between species in orientation of mucosal folds and variation in distribution of certain cell types. He also noted the lack of a "portio cardiaque" in the insect-eating *Nyctimene cephalotes,* a structure characteristically present in fruit-eating megachiropterans. Grassé (1955) reiterated the basic classification of Robin, and additionally noted differences between the vampire genera *Desmodus* and *Diphylla* in the lengths of the caecal pouches, and that the distribution and structure of gastric glands were notably different in *Desmodus* from those of other bats.

Several early authors, notably Rollett (1871) and Langley (1880-82), described the structure of the gastric mucosa of bats, but, unfortunately, neglected to name the kinds examined. Langley noted that the fundic glands were generally short, that those of the greater curvature were especially long, that parietal cells were relatively few in number, and, although perhaps unwittingly, was probably the first to describe a pylo-fundic transition zone. His observations seem to agree well with those included here for *Plecotus townsendii.* Rollett's study was similar to Langley's, although Rollett claimed to have observed reduced numbers of "adelomorphous" or border cells in summer-taken as opposed to winter-taken specimens. Present evidence questions the reliability of these findings.

Until relatively recently, the bulk of investigation concerning gastrointestinal structure in the Chiroptera was almost entirely macroscopic in nature. Several noteworthy earlier papers deserve consideration. Mathis (1928a), in an extensive treatise restricted to a discussion of the intestinal portion of the digestive tract, described the patterns of intestinal folds and selected glandular areas in the intestines of nine species of bats, and noted differences in intestinal length and relationships between patterns of intestinal folds and types of nutrition. Eisentraut (1950) noted that among the species he examined the stomachs of insect-eaters tended to be simpler and less saccular than those of the megachiropteran fruit-eaters, and that the tendency toward the development of an extensive blind-ended, saccular fundic caecum could be found only in the Phyllostomatidae of the Microchiroptera. He also noted that two glossophagine bats, *Glossophaga* and *Choeronycteris,* had stomachs that closely resembled the condition in insect-eating vespertilionid and emballonurid species. However, Eisentraut's illustrations of stomachs of some species strongly suggest that they were distended and therefore not typical of the "empty" condition; his drawings of stomachs of *Carollia* and *Artibeus* are, however, nearly identical to those included for these genera herein. Fischer (1909) established that the mucous membrane was better developed in the cranial than the caudal portion of

the stomach. The same was stated for the musculature, but, unfortunately, no reference was made as to the species examined. Fischer held that a condition of localized hypertrophied mucous membrane and musculature was traceable to an adaptation to eating hard insects. Kolb (1954) examined stomachs of *Rhinolophus, Nyctalus,* and Old World *Eptesicus,* and considered reductions and specializations of certain portions of the gastric mucosa in these bats in relation to diets predominantly composed of insects. Kolb concluded that specializations such as folding of the stratified epithelium at the gastroesophageal junction, greater development of the musculature and gastric mucosa in the lesser as opposed to the greater curvature (as noted by Fischer, 1909), and secondary reduction of gastric mucosa in the blind end of the caecum were in some way related to insectivorous feeding habits, or to protection of the mucosal membrane from abrasion by chitinous fragments.

Park and Hall (1951) examined the tongues and stomachs of eight species of New World bats, commenting on the apparent specializations in both tongue and stomach to incorporate a heavily liquid diet in *Desmodus.*

Studies that deal specifically with the histological structure of the gastrointestinal tract of bats are few, and even fewer are comparative in approach. Fischer (1909) examined microscopic sections of the gastrointestinal wall, showing for *Barbastella* and *Vespertilio* that the musculature was thicker within the lesser curvature. Fischer was the first worker to examine in detail the gastroesophageal junction (*Barbastella*). He noted that the junction between the esophageal epithelium and gastric mucosa was abrupt and described a local thickening of the circular muscle layer at the junction similar to that described herein for *Rhynchonycteris naso.* Mathis (1928b) examined the cellular structure of the glands of Brunner of three vespertilionid species and a rhinolophid. He observed in all cases a clear-cut distinction in cellular morphology between the glands of Brunner and the pyloric glands. Mathis noted slight differences in Brunner's glands in different species; his figure of the pyloric junction in *Vesperugo* (=*Pipistrellus*) *pipistrellus* is notably similar to that of *Plecotus* included here. Kolb (1954) examined the cardiac glands of two bats (probably *Nyctalus* and *Rhinolophus*), concluding that they probably functioned as a source of lubricant for materials entering the stomach, and also observed in *Rhinolophus hipposideros* that the cardiac glands penetrated the lower esophageal epithelium within a narrow belt at the glastroesophageal junction. An especially important recent contribution is that of Schultz, 1970. This paper proposes familial status for a megachiropteran, *Harpionycteris whiteheadi,* based on studies of gastrointestinal structure.

A recent paper by Rouk and Glass (1970) presents comparative accounts of gastric structure in five species of North American bats, and reviews additional pertinent literature not referred to here.

Two significant contributions concerning comparative gastrointestinal morphology, although not specifically considering chiropteran anatomy, are those of Allison (1948) and Myrcha (1967) on the Insectivora. These papers include comprehensive accounts of gross gastric morphology of both Old and New World insectivores, and I have referred to them occasionally for comparative purposes, because the Insectivora and Chiroptera are basically similar in several aspects of gross gastric structure.

Histochemical examination of intestinal sections was undertaken in an attempt to examine the qualitative and quantitative nature of mucopolysaccharides in the gastric mucosa and the submucosal glands of Brunner. Owing to the limited amount of material available for these studies, and to the nature of the fixatives employed, only a few techniques were used and the study must be regarded as preliminary in nature. Longitudinal sections of stomachs examined histologically were included in all mucin reactions when possible.

Prior to the relatively recent development of procedures for differentially staining and identifying mucous substances, it long had been recognized that mucins of various cells of the gastrointestinal epithelium reacted differently, and that differences in staining properties of the same cell type could be found in different species. Clara (1940) noted staining differences between types of mucous cells specifically with reference to stomachs of different species, and Liebermann (1887-88, as cited by Jennings and Florey, 1956) had previously suggested, on the basis of chemical investigations on extracts of mucosa, that different kinds of mucin were present in mammalian stomachs. Liebermann categorized mucins into those that contained sulphur, and those that did not. It is of some interest to note that present-day classifications of mucopolysaccharides (see Spicer, 1963) employ the condition of the presence or absence of sulfate radicals. A few workers, including Clara (1940) and Gomori (1952), have suggested that gastrointestinal mucins may be distinguished as either true mucin or mucoid on both histological and histochemical grounds, although different techniques of fixation and staining apparently yield inconclusive results (Järvi and Laurén, 1951). A comprehensive review and summary of the best known and most widely used procedures for characterizing mammalian mucopolysaccharides is that of Spicer (1963).

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MATERIALS AND METHODS

Whole gastrointestinal tracts of bats were taken from specimens collected in nets or shot during crepuscular feeding, and, in one case *(Plecotus townsendii)*, from torpid individuals taken in a winter hibernaculum. Most tropical species were netted, and usually were fasted for a minimum of 10 hours. A total of 28 stomachs, chosen because they were adequately preserved and devoid of gastric contents, were used for histological and histochemical examination. An additional 12 specimens, including one of *Noctilio leporinus* (a species of which I had no suitable specimens) were examined only macroscopically. Specimens listed as examined were those sectioned and stained. Descriptions of topography include observations made on non-sectioned material, whereas the recorded measurements are only from stomachs prepared for histological examination.

The exact physiological state of specimens at the time of preservation is unknown, although, if used for histological examination, specimens had stomachs devoid of gastric contents.

All material was fixed in either Bouin's or 8% formalin in the ratio of at least 10 parts fixative to one part tissue by volume, and subsequently preserved in 70% ethyl alcohol. Several stomachs from specimens preserved in spirits as museum specimens were sectioned and stained with hematoxylin and eosin, but judged unsuitable for microscopic study.

Material was imbedded in 52.0° Tissuemat and sectioned frontally at 5-7 microns. The following histological techniques were employed:

1) Harris' hematoxylin and eosin (Harris' formula after Davenport, 1960).

2) Mallory's triple connective tissue stain (Pantin, 1948).

The following histochemical procedures were used:

1) Toluidine blue O (Lillie, 1965).—A 1:1000 aqueous solution was employed with exposure for 15 seconds with immediate transfer to acetone.

2) Steedman's Alcian blue 8GX for mucins (Steedman, in Lillie, 1965).—Alcian blue 8GX 300 (Allied Chemical Co.) was employed for 60 seconds with a distilled water rinse. This procedure employs an aqueous solution of the dye and was used at a pH of 7.1.

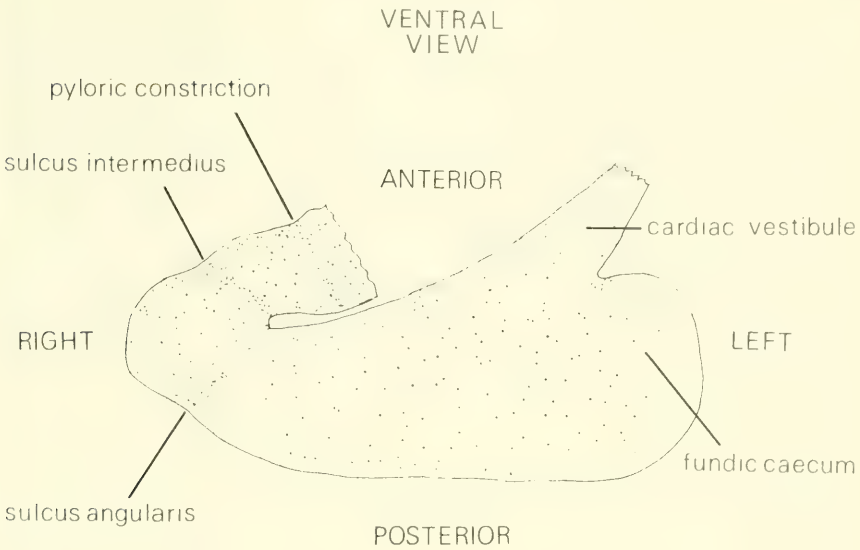
3) Maxwell's periodic acid Alcian blue for gastric mucus (Maxwell, in Lillie, 1965). This procedure, which employs exposure of sections to periodic acid oxidation prior to staining was used as a supplement to Steedman's method, and as an additional check for glycogen.

4) Periodic Acid Schiff sulfite leucofuchsin reaction (Lillie, 1965). Control slides (no exposure to periodic acid) also were employed.

In addition to successful histochemical procedures described above, several other types were attempted, but did not provide conclusive results. One of these was digestion with testicular hyaluronidase, followed by toluidine blue O (Lillie, 1965). Sections exposed to 18 hours digestion in 1:10,000 aqueous hyaluronidase at 37°C revealed no distinguishable alteration of toluidine blue metachromasia in comparison to control sections, therefore yielding negative results in a test for chondromucins and hyaluronic acid.

The two Alcian blue procedures were run as single series, one with, and one without, periodic acid oxidation prior to staining. The toluidine blue O procedure was carried out twice, once as a single series, then as a control series for the hyaluronidase lysis.

Scoring of the intensity of Alcian blue and PAS reactions was as follows: exceptionally strong (++++), moderately strong (+++), moderate (++), weak (+), barely perceptible (trace), not observed (—). Toluidine blue O was scored simply as plus (+), the presence of demonstrable metachromasia, and minus (—), metachromasia not observed.



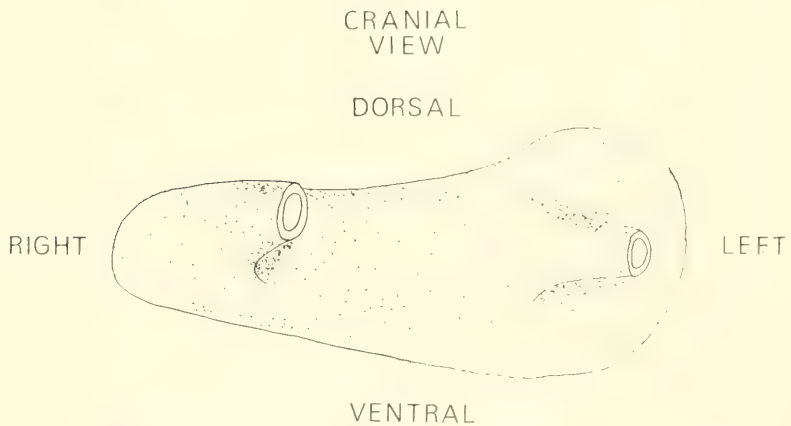


FIG. 1 (upper). Diagrammatic representation of the stomach of *Carollia perspicillata* (ventral view). Note the location of various sulci.

FIG. 2. (lower). Stomach of *C. perspicillata* (diagrammatic), viewed cranially.

Anatomical terminology and descriptions of location and direction of parts used with reference to the gastrointestinal tract frequently are undefined or unclear, sometimes inappropriate, and otherwise variously misused in the literature. For these reasons, a list of defined terms is included here in addition to the brief discussion of orientational terminology to follow.

All descriptions and discussions of gastric morphology are based on location of the stomach *in situ* in the abdominal cavity. Anterior (craniad) and posterior (caudad) are here considered those directions of the lesser and greater curvatures, respectively (Fig. 1), usually con-

sidered dorsal and ventral, respectively, in the literature. Dorsal is here considered that surface of the stomach nearest the vertebral column, whereas ventral is that surface farthest from (or opposite to) the vertebral column (Fig. 2). All gastric structures are distal to the apex of the fundic caecum, and likewise proximal to the pyloric sphincter.

All measurements of gross structures are in millimeters, and are included to give an indication of stomach size and orientation of various features with respect to others. Measurements of depths of the various zones of gastric mucosa were obtained using a dial micrometer. The ranges are recorded in microns.

All photographs are of structures stained with Harris' haematoxylin and eosin unless otherwise indicated.

Mid-longitudinal outline drawings represent composites of specimens of each species, and were produced by projecting representative sections onto paper using a photographic enlarger, tracing the outlines for each specimen, and producing a composite outline by means of a light table. Within some mid-longitudinal drawings, structures not observed in medial sections, although important enough to be included in the illustrations, are depicted by broken lines.

Uncommon morphological terms used in the accounts that follow are listed and defined below.

Cardia.—Limited area of stomach surrounding gastroesophageal junction.

Cardiac vestibule (same as cardia).—Part of stomach between gastroesophageal junction and general plane of lesser curvature.

Elastic stomach.—That region of the stomach lateral to gastroesophageal junction terminating in a blind end, usually containing some elastic fibers.

Fundic caecum.—Generally, area between gastroesophageal junction and left lateral terminus of stomach.

Fundus.—That part of the stomach that secretes acid and pepsin, lying between cardiac and pyloric parts.

Incisura cardiaca.—Notch formed between cardiac vestibule and fundic caecum at entrance of esophagus into stomach.

Pyloric constriction.—External furrow at pyloric sphincter.

Pyloric bend.—Cranial recurvature or arching of terminal stomach.

Pylorus.—Glandular region of stomach composed entirely of cells resembling mucoid neck cells, located proximal to pyloric sphincter.

Saccular stomach.—That portion between gastroesophageal junction and apex of fundic caecum.

Sulcus angularis.—Furrow (external) formed generally at, or slightly proximal to, pyloric bend.

Sulcus intermedius.—Furrow (external) approximately midway between pyloric bend and pyloric sphincter.

Terminal stomach.—That portion between gastroesophageal junction and pyloric sphincter.

Transition zone.—Zone of transitional gastric glands between fundic mucosa and other glandular types.

ACCOUNT OF SPECIES

The gastrointestinal tracts of all Chiroptera examined consisted of the same typical segments that have been described for other kinds of mammals: a thin-walled, extremely narrow esophagus lacking submucosal or mucosal glands and lined entirely with stratified squamous epithelium, within which the usual four strata of squamous cells could be observed; a distinctive, saclike, muscular stomach (with the exception of the blind tube of *Desmodus rotundus*) completely lined with well-differentiated, usually simple, branched, tubular mucosal glands which are differentiated by the occurrence of particular cell types and identifiable within specific zones; a relatively long small intestine (especially long in *Desmodus*) with thin, muscular

walls, little loose submucosal tissue, and long, narrow villi; and a well-developed colon including numerous goblet cells and somewhat more extensive non-muscular submucosa than the small intestine.

The wall of the chiropteran stomach is composed of the tunica mucosa, tunica submucosa, tunica muscularis, and tunica serosa. Tunica serosa lines the entire external surface of the stomach; no squamous tissue is present except in the uppermost portion of the cardiac vestibule of *Natalus stramineus*. The amount of non-muscular submucosa in the stomachs of most bats examined was found to be extremely small in comparison to many other mammals. Infrequent to numerous accumulations of lymphatic tissue within the tunica propria were observed in some, but not all, specimens. Vascularization of the tunica propria was similar in all species examined with the exception of *Desmodus rotundus*, in which the complements of arterioles and venules are extensive.

In all species the tunica mucosa, submucosa, and thin sheet of smooth muscularis mucosa just beneath the gastric glands are thrown into longitudinal or transverse (or both) and anastomosing rugae. These rugae, few to many depending on the species, extend throughout the stomach, terminating at the gastroesophageal and pylo-duodenal junctions. Rugae may or may not be reduced at the apex of the elastic stomach (fundic caecum), and are often poorly defined in a fully distended stomach. The tunica muscularis proper consists of an inner circular and outer longitudinal layer, with extensive variation in depths of layers in various species. A third, extremely thin layer of smooth muscle fibers lies to the inside of, and oblique to, the two outer layers, usually separated from them by a thin zone of loose submucosal tissue.

In all species examined, I noted a partial or pronounced cranial recurvature of the aboral end of the stomach, often beginning substantially proximal to the pyloric sphincter (*Natalus* perhaps an exception). This condition has been observed in other species of bats, including members of the Megachiroptera, and immediately distinguishes stomachs of Chiroptera from many members of the Insectivora, notably soricids examined by Myrcha (1967). Curvature of the stomach is known in some Insectivora (Erinaceidae, Talpidae) and its significance as a diagnostic character in the Chiroptera will be discussed later.

All species examined (except *Desmodus*) have four distinctively recognizable zones of gastric mucosa—cardiac, fundic, pylo-fundic transition, and pyloric. Although *Desmodus* may in fact have all four zones represented, mucous glands occupying the area between oral and aboral orifices of the stomach are identical and are here considered to be pyloric glands. Cardiac glands are mucus-producing and appear to contain a single cell type. Fundic mucosa usually occupies the majority of the inner surface area and is com-

posted of tubular glands containing mostly zymogenic cells that are the proposed sites of pepsin secretion, parietal cells that secrete hydrochloric acid, and various mucus-producing cells. The transitional zone is a highly variable area, both dimensionally and structurally, representing the change from fundic to pyloric mucosa within the terminal stomach. The pyloric zone, always proximal to the pyloric sphincter, is a second mucus-producing area composed of relatively straight tubular glands with a single cell type.

The stomach of the vespertilionid *Plecotus townsendii* was considered to be relatively generalized among bats examined. Because of its notable symmetry and seeming lack of unusual specialization, the stomach is often used in the accounts in comparison or contrast to structures in other species where clarity by means of comparison appeared necessary. Species are arranged in the following accounts in phylogenetic order following Hall and Kelson (1959).

Due to the small sample sizes of species employed in this study, the conclusions drawn here must be regarded as preliminary, and the study of a pilot nature. Further study utilizing many more specimens is encouraged, in order to document intraspecific variation.

Family EMBALLONURIDAE

Rhynchonycteris naso (Wied-Neuwied, 1820)

Specimens examined (2).—Two specimens from Nicaragua (KU 105911, 105915).

Overall dimensions.—Greatest length 7.4-8.1; greatest breadth 3.1-3.8; gastroesophageal junction to pyloric sphincter 2.4-2.9; gastroesophageal junction to apex of fundic caecum 2.5-2.8; breadth pylorus at sphincter 1.3-1.4.

General morphology.—Stomach tubular, reniform, generally symmetrical although tapering gradually throughout from fundic caecum to pylorus; pronounced curvature in frontal plane throughout body with apex of fundic caecum directed antero-laterad; tubular stomach gradually curved anteriad two-thirds distance from apex of fundic caecum to pyloric sphincter, continuing craniad as narrow, relatively long, tubular endpiece directed cranially and parallel to cardiac vestibule; lesser and greater curvatures nearly parallel throughout; terminal endpiece lateral to pyloric curvature largest among insectivorous species examined; stomach rounded on sides, convex on both dorsal and ventral surfaces. Cardiac vestibule present although short and narrow, musculature of wall well developed as through much of lesser curvature; vestibule at marked angle to lesser curvature and relatively uniform in breadth with little expansion posteriorly; incisura cardiaca relatively deep and narrow, created by marked angle of cardiac vestibule to lesser curvature; distinctive local thickening of both longitudinal and circular muscle layers within incisura, but no apparent separation of circular

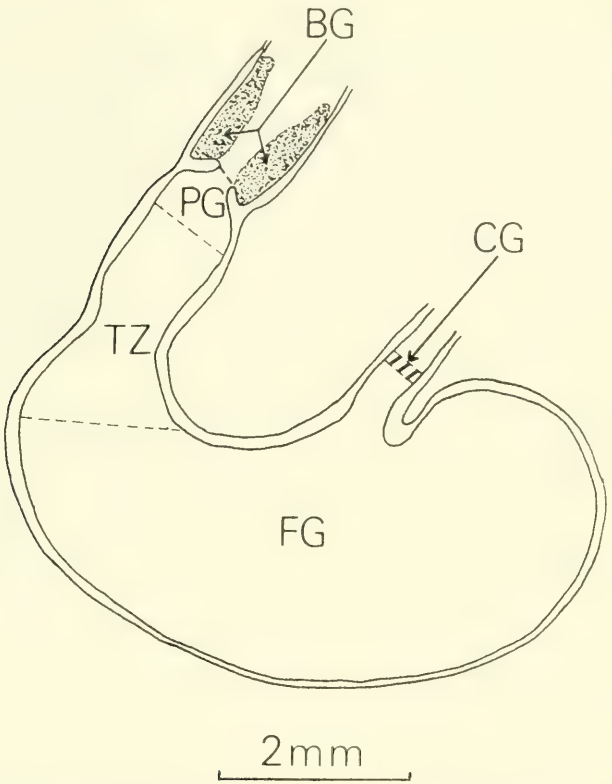


FIG. 3. Mid-longitudinal representation of the stomach of *Rhynchonycteris naso*. Explanation of symbols: **CG,** zone of cardiac glands; **BG,** zone of Brunner's glands; **PG,** zone of pyloric glands; **TZ,** transitional zone; **FG,** zone of fundic glands.

fibers into laminated sheets at incisura; additional local thickening of circular muscle layer within cardiac vestibule opposite incisura cardiaca, possibly forming anatomical cardiac sphincter (Fig. 3) (see discussion of musculature). Fundic caecum well developed, dilated, expanded superiorly and with surface rounded throughout; structurally continuous with midstomach (not anatomically distinctive chamber), oriented longitudinally on dorsal surface (no dorsal hook). Terminal stomach distal to cardiac vestibule long, decreasing gradually in breadth to just beyond midpoint where prominent sulcus intermedius distinguishes proximal funnel-like portion from narrow, relatively long terminal endpiece (2.5 mm in length); terminus lateral to sulcus recurved slightly, nearly parallel to cardiac vestibule, uniform in breadth to pyloric sphincter. Pyloric sphincter long and narrow, valves of equal length as measured on lesser and greater curvatures; expanded through medial half to appear narrowly spoon-shaped in cross-

section; differing from that of other bats examined in being equivalent in depth to circular muscle of pyloric tube that gives rise to sphincter within both lesser and greater curvatures; valve aperture narrow. Pyloric junction slightly superior to gastroesophageal junction *in situ*. Musculature generally thin throughout much of stomach wall, thickened locally; unusual arrangement of circular layer in lesser curvature. Rugal folds numerous, reduction of mucosal lining throughout relatively large portion of fundic caecum and greater curvatures. Lamina propria mucosae extremely thin except within fundic caecum and portions of terminal endpiece of terminal stomach. Glands of Brunner moderately abundant. Stomach conforming in most features to general configuration common to other obligate insectivorous bats.

Musculature.—Typical three layers observed in both specimens. Longitudinal layer a simple thin sheet throughout most of stomach, locally thickened 1) in incisura cardiaca where there is substantial increase in depth within the depression, 2) throughout longitudinal zone of fundic caecum where it is somewhat thicker than overlying circular layer through much of caecal region, and 3) in the mid-region of terminal stomach on greater curvature. Circular muscle relatively narrow throughout pyloric tube in comparison to other bats examined, uniform in depth throughout length of pyloric tube as well as equal in depth in lesser and greater curvatures; circular layer locally thickened within broad area in lesser curvature immediately opposite incisura cardiaca, equivalent in depth to that of incisura and extending from midpoint between gastroesophageal junction and sulcus intermedius to just beneath gastroesophageal junction, resulting in "ring" of thickened musculature at lower end of cardiac vestibule, an anatomically plausible cardiac sphincter inferior to gastroesophageal junction although clearly not a valvular closure mechanism; circular layer extremely thin through fundic caecum and majority of greater curvature, shallower than longitudinal layer; bundling of circular muscle occurring only in zone of greater curvature proximal to pyloric bend. Muscularis mucosae typical, thickest at incisura cardiaca and in fundic caecum. Lamina propria mucosae (beneath muscularis mucosae) abundant only in fundic caecum. Depth of longitudinal layer 15 to 100 (incisura cardiaca), depth of circular layer 15 to 140 (incisura cardiaca and opposing wall), depth of muscularis mucosae 15 to 25.

Organization of gastric mucosa.—Rugal folds deepest and most abundant within tubular portion, originating at pyloric sphincter and radiating into mid-stomach, becoming progressively more widely spaced as tube expands; frequency of folds constant through tubular portion; least number of folds originating along lesser curvature from pyloric bend to cardiac vestibule, consistently directed toward lower apex of fundic caecum; upper wall of

caecum (lesser curvature) with relatively frequent, short, transversely-directed rugae extending downward to mid-region of dorsal and ventral surfaces of caecum; folds well developed and longitudinal within cardiac vestibule; major portion of greater curvature and all of lateral wall of fundic caecum lacking prominent rugal folds (gastric mucosa also distinctively reduced in depth), which originate in pyloric tube and along lesser curvature and terminate in lower middle area of ventral and dorsal surfaces of body of stomach; resulting pattern that of transverse to progressively more longitudinally directed rugae from caecum to pyloric tube through approximately upper three-fourths of body of stomach and all of tubular stomach. All mucosal gland types represented; cardiac and pyloric zones relatively short, fundic mucosa occupying remaining surface area except for unusually broad transitional zone occurring through nearly all of pyloric tube; no Brunner's glands within gastric mucosa. Progressive decrease in mucosal depth from middle fundus through transitional zone and pyloric glands to pyloric sphincter with slight secondary increase within terminal pyloric mucosa, cardiac glands comparable in depth to transitional zone; deepest mucosa within lesser curvature of fundus; glands within apex of fundic caecum and in the basal, non-tubular portion of greater curvature reduced in length.

Cardiac glands.—Zone of true cardiac glands extremely narrow; transitional zone to fundic mucosa slightly longer than cardiac zone; cardiac glands short and broad, composed of single type of cell although some local variation in morphology of nuclei occurring within gland; cells within bulbous base small, elongate, with giant spherical nuclei; upper cells smaller, more cuboidal with nuclei decreasing progressively in size although remaining spherical throughout to epithelium; lumen broad, increasing only slightly in breadth toward surface; epithelium in small clumps between adjacent glands because luminal openings of glands broad and close together, cells elongate, nuclei compressed laterally. Transitional zone to fundic mucosa with numerous (but scattered) parietal cells throughout length of glands. Interglandular and basal lamina propria no more abundant than within fundic zone. Depth of cardiac mucosa 160 to 170.

Fundus.—Most variable in structure of all bats examined; true simple tubular glands of branched type only within upper three-fourths of stomach, reduced (dwarfed) to thin layers of oxnyctic, chief and mucous neck cells within lower fourth (including much of fundic caecum); glands deepest between fundo-pyloric bend and medial limit of fundic caecum (inclusive of cardiac vestibule), moderate in depth within most of tubular stomach, decreasing slightly into transitional zone; reduction of glands within lower fundus resulting from general reduction, sometimes complete loss, of one or more cell types characteristic of fundic mucosa. Depth of fundic glands

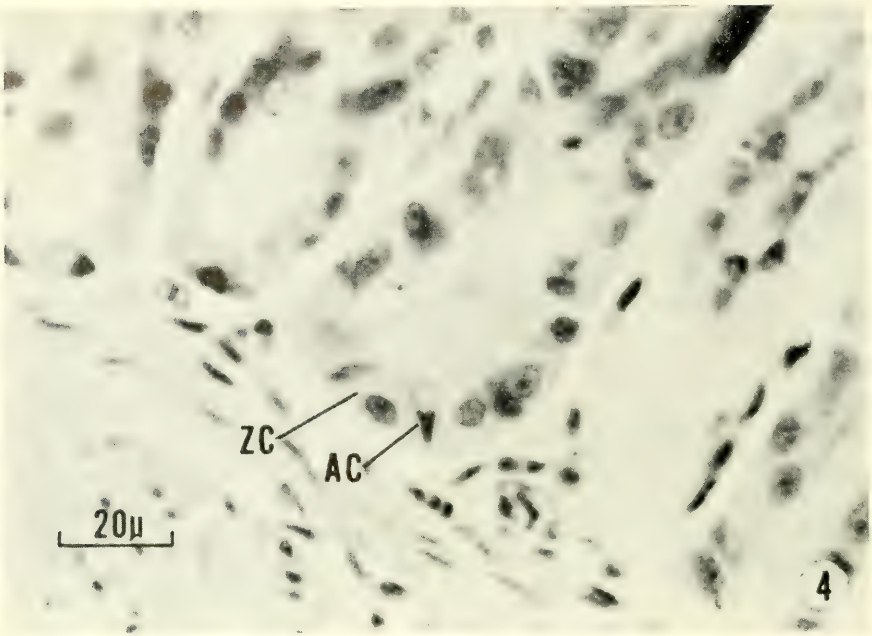


FIG. 4. Argentaffin cell (**AC**) at base of fundic gland of *Rhynchonycteris naso*. **ZC**, zymogenic cell.

180 to 220 within lesser curvature, cardiac vestibule, part of fundic caecum, and zone beneath transitional area within greater curvature; 40 to 100 within zone of dwarfed glands.

Zymogenic cells occupying only lower fifth of gland, most abundantly concentrated in stomach within lesser curvature and tubular portion of greater curvature, and only scattered infrequent basal elements through most of remaining area; zymogenic cells small, pyramidal, largest within expanded basal arc, decreasing in size and becoming more elongate within upper area of intraglandular distribution; nuclei of zymogenic cells small, spherical, and juxtaposed to basal membrane.

Argentaffin cells (Fig. 4) observed infrequently, usually among parietal instead of chief cells, approximately same size as mucous neck cells, being extremely narrow, triangular, and with nucleus at inner border; point of triangle peripheral; nucleus extremely small, spherical, dense argentaffin granules lateral (Fig. 4).

Parietal cells abundant within upper 75% of glands throughout lesser curvature from upper midpoint of fundic caecum to pylo-fundic transition; also common through small area of lesser curvature just beneath transitional zone, extremely sparse to absent through most of greater curvature; parietal cells highly variable in size, distinctive intraglandular size gradient with

increase from bottom to top of distribution, uppermost cells extremely large; cells most densely distributed just beneath necks of gastric pits where unbroken rows of five to seven often observed, rarely found among chief cells; sparsely distributed in greater curvature and generally smaller there than in areas of abundance; usually ovoid.

Mucous neck cells extremely small as compared to adjacent parietal cells; rarely occurring singly, usually observed in clumps of four or five, most often situated along inner margin of tubule; nucleus half size of parietal cell nuclei, oblong, irregular in shape, and with little cytoplasm; mucous neck cells composing most of cellular complement within stunted glands of greater curvature and fundic caecum in absence of many chief and parietal cells.

Gastric pits shallow through lesser curvature (15-20% length of glands), extending to base within dwarfed glands of greater curvature in absence of non-mucoid cellular elements; cells lining pits similar to lower mucous neck cells, although lumenal mucous border moderate in depth; no prominent lateral flattening of nuclei within lesser curvature although neck cell nuclei compressed within dwarfed glands of lower stomach; surface epithelium thick, nuclei typically basal, club-shaped, and twice length and breadth of gastric pit nuclei; interglandular and basal lamina propria extremely sparse.

Pylo-fundic transition zone.—Extensive area; parietal cells persisting through terminal endpiece nearly to pyloric sphincter, resulting in extremely narrow pyloric zone; zymogenic cells gradually reduced in number from initial margin of zone, large numbers of mucous cells occurring basally with parietal cells throughout zone; loss of parietal cells along terminal border of zone also gradual, with persisting cells at aboral margin usually basal within glands; increase in depth of gastric pits progressive along with loss of parietal elements, beginning in midregion of transition; slight reduction in depth from fundic mucosa; depth of transitional mucosa approximately 150.

Pyloric glands.—Pyloric mucosa confined to extremely narrow area at pyloric sphincter owing to extensive aboral advancement of parietal cells; glands short and broad, equivalent in breadth to fundic glands; cells within basal third elongate and narrow, with extremely small, spherical, basal nuclei; cells within middle third more globular, nuclei twice size as those of basal cells and ovoid, upper cells becoming progressively broader and shallower toward surface epithelium with nuclei increasing correspondingly in degree of lateral compression; glands relatively uniform in depth and breadth throughout distribution, basal fourth of tubule expanded into bulb, remaining portion uniform in diameter to surface epithelium; lumen narrowest within bulb, increasing gradually in breadth to surface; surface epi-

thelium is in small clumps as orifices are broad and close together, cells narrow, elongate with similarly shaped nuclei; loose lamina propria more abundant beneath pyloric mucosa than fundic, typically sparse between glands; depth of pyloric mucosa 150 to 170.

Glands of Brunner.—Confined to short, although broad, massive ring occupying only proximal 1.0 mm of duodenum; deepest along distal surface of pyloric sphincter, decreasing sharply distally; tubules moderate in breadth, cross-sectional morphology identical to that of most other bats examined except nuclei extremely small, juxtaposed to basement membrane, and perfectly spherical; glands restricted to duodenum, always submucosal.

Remarks.—The antero-posteriorly expanded tubular stomach of *Rhynchonycteris* is well representative of the "insectivorous" condition, with a few noteworthy specializations.

The musculature is substantially better developed on the lesser, as compared to the greater, curvature, a characteristic unique to this species. This condition is greatest at the gastroesophageal junction where local thickening occurs, suggestive (although not conclusively indicative) of the presence of a non-valvular cardiac closure mechanism. Continuation and expansion of the work of Botha (1958, a-c) on gastroesophageal closure mechanisms in mammals would be enlightening in this regard.

The pattern of gathering of the mucosal folds is unique in two respects. Many rugae originate along the lesser curvature and are directed somewhat downward, toward the lower apex of the fundic caecum, rather than strictly longitudinally as in other obligate carnivores. Also, although not unique among carnivorous bats (observed to some extent in *Plecotus townsendii* in this study), transversely directed rugae are much in evidence within the upper fundic caecum. Secondly, unparalleled reduction of mucosal folds and depth of glands occurs throughout much of the greater curvature.

The gastric mucosa is unique in its impoverished complement of zymogenic cells within the fundic zone (excepting the overall reduction of the gastric mucosa in *Desmodus*). The transitional zone is extensive in terms of length and parallels that of *Pteronotus* in being not only a distinctive portion of the mucosa, but by limiting the pyloric mucosa to an extremely narrow band at the pyloric sphincter.

Family NOCTILIONIDAE

Noctilio labialis (Kerr, 1792)

Specimens examined (2).—Two specimens from Nicaragua of *Noctilio labialis minor* (KU 105941, 116690).

Overall dimensions.—Greatest length 12.9-13.5; greatest breadth 7.0-8.0; gastroesophageal junction to pyloric sphincter 5.8-6.1; gastroesophageal junction to fundic caecum 4.4-4.7; breadth pylorus at sphincter 2.4-2.6.

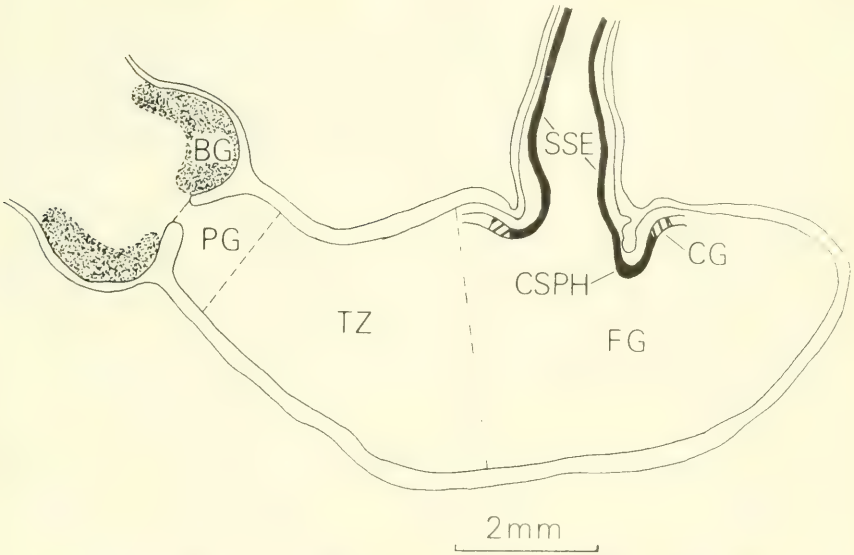


Fig. 5. Mid-longitudinal representation of the stomach of *Noctilio labialis;* **SSE,** stratified squamous epithelium; **CSPH,** cardiac sphincter. For explanation of other symbols, see Figure 3.

General morphology.—Stomach tubular, relatively short and narrow, only slightly curved in frontal plane; lesser curvature arched anteriorly; anterior and posterior surfaces of stomach convex resulting in egg-shaped stomach. Fundic caecum short and narrow, tapering to narrow apex, directed laterally, not chambered. Esophagus entering stomach at slight angle; cardiac vestibule lacking gastric mucosa, stratified squamous epithelium extending posteriorly beyond arc of lesser curvature forming lip at entrance of esophagus into stomach, and incorporated as lining of well-developed cardiac sphincter of mixed type as defined by Botha (1958 a,b); sphincter composed of both striated and smooth muscle elements.

Cardiac sphincter occurring as distinctive fold of stomach wall (Figs. 5-6) at entrance of esophagus into stomach, asymmetrical, best developed on pyloric side; composed of circular muscle layer, muscularis mucosae and surrounding lamina propria, and stratified squamous epithelium, but longitudinal muscle layer not incorporated into fold; circular muscle projecting downward to apex of lip and recurving sharply craniad to lesser curvature, subdivided into extensive numbers of laminated sheets, nearly uniform in breadth throughout junction; muscularis mucosae extensive throughout sphincter, fibers separating into radiating bundles at apex of lip, continuing as narrow double layer at onset of gastric mucosa; most of sphincter lip lined with thin, rugose layer of esophageal epithelium, lateral edge of lip

partially lined with gastric glands; loose connective tissue abundant above and below muscularis mucosae within that portion of lip lined with squamous epithelium. Prominent external constriction at junction of abdominal esophagus and gastric sac, incisura cardiaca absent, cardiac orifice broad; squamous epithelium at cardiac junction and adjacent cardiac mucosa similar in depth.

Terminal stomach distal to cardiac junction moderate in length, curved relatively slightly craniad, tapering gradually to sphincter; pyloric bend slight; orifice at sphincter narrow because flaps of sphincter long; external pyloric constriction prominent, partly owing to extensive expansion laterally within duodenum of submucosal glands of Brunner; musculature of pyloric sphincter narrow, flaps relatively long, longer and broader on greater than lesser curvature; circular muscle layer of duodenum sole muscular contribution to sphincter as circular layer discontinuous from pylorus to duodenum with pyloric complement ending abruptly at sphincter; sulcus intermedius present and well developed approximately 2 mm proximal to pyloric sphincter; sulcus angularis occurring midway within terminal stomach. Pyloric and cardiac orifices at approximately equivalent levels but not unidirectional. Lamina propria mucosae abundant and dense within rugae, less abundant, although prominent beneath muscularis mucosae of outer wall. Rugal folds extensive in number and depth throughout stomach, unusually prominent through portions of greater curvature; gastric mucosa moderate in depth, showing familiar pattern of reduction in depth between folds.

Musculature—Musculature generally deep throughout stomach, best developed within most of greater curvature and terminal 3 mm of lesser curvature. Longitudinal layer a thin sheet throughout all of lesser curvature and cardiac junction, abruptly thickened and moderate in depth throughout fundic caecum; locally thickened to prominent layer through medial 4 mm of greater curvature, again narrowing and remaining narrow through terminal portion of greater curvature to pyloric sphincter. Circular layer relatively narrow through fundic caecum, locally thickened within medial portion of greater curvature (along with underlying layer), again narrowing just proximal to sulcus intermedius where local thickening of circular layer only is present, narrowing again before increasing sharply in breadth to pyloric sphincter; correspondingly thickened zones between cardiac junction and pyloric sphincter within lesser curvature, although locally thickened areas slightly deeper; gathering of circular fibers into bundles extreme in, and restricted to, fundic caecum and greater curvature laterally through thickened midregion. Muscularis mucosae typically thin layers within stomach wall, slightly thicker within rugae, most prominent at cardiac junction. Ganglia of Auerbach's plexus more abundant within greater curvature than in lesser curvature. Depth of longitudinal layer

30 to 60, circular layer 30 to 90 (caecum) to 300 (pyloric tube), muscularis mucosae less than 10 up to 20.

Organization of gastric mucosa.—Mucosa gathered into longitudinal parallel ridges from apex of fundic caecum to pyloric sphincter; rugal folds best developed of any bat examined; shallow within caecum, increasing gradually in depth from origin in fundic caecum through midstomach, decreasing again into pylorus; folds gradually decreasing in length and increasing in depth from lesser curvature posteriad to greater arc. Folds within medial half of greater curvature longitudinally directed, relatively short finger-like projections of tremendous depth (up to 3.5 mm) directed anteriorly into gastric lumen; few folds originating from lesser curvature (only within upper wall of fundic caecum). No transversely oriented rugae; moderately developed "zig-zag" configuration in folds within posterior three-fourths (absent within region of lesser curvature) from apex of fundic caecum to sulcus intermedius, never truly interdigitating; folds shallow, infrequent at gastroesophageal junction. Mucosa shallowest in depth at gastroesophageal junction, uniform in depth throughout remaining stomach excepting slight reduction within interrugal furrows in comparison to sides and apexes of rugae; no appreciable reduction within (or at apex of) fundic caecum; deepest mucosal glands on sides of rugae within terminal portion of transitional zone.

Zones of gastric mucosa atypical among carnivorous types examined, apparently accounting for extremely large transition zone, cardiac glands occupying typically narrow band at gastroesophageal junction, equivalent in breadth throughout; true fundic mucosa restricted to approximately left half, inclusive of region of cardiac junction; transitional zone to pyloric mucosa occupying most of terminal half, thus limiting true pyloric glands to narrow belt at sphincter; all zones relatively symmetrical regarding length of distribution on lesser and greater curvatures (Fig. 5).

Cardiac glands.—Zone of cardiac glands in complete absence of parietal cells, extremely narrow; glands short and broad relative to remaining mucosal elements; single cell type apparently present but extensive morphological variation within tubules; cells within basal fourth small and many with extremely large, centrally located nuclei; cells in upper three-fourths of tubule becoming progressively larger, more elongate, with increasingly small, more ovoid nuclei toward upper limit of tubule; tubules not highly convoluted, bases usually although not always bulbous and uniform in breadth through upper portion; lumen moderate in breadth, slightly broader at base than neck; smooth muscle fibers and areolar connective tissue more abundant beneath and between tubules than in other mucosal areas; surface epithelium thin, cells narrow with large ovoid nuclei located in lower middle portion; depth 120 to 140.

Fundus.—Relatively restricted fundic zone characterized by marked uniformity in depth and morphology of glands; deepest glands within midstomach, decreasing only slightly toward apex of fundic caecum, slightly reduced in depth within furrows. Consistent zonation of cellular elements within fundic glands with little variation in length of zones throughout; lower 30% restricted to zymogenic cells with occasional rare argentaffin cell; middle 40% occupied by numerous parietal cells with less abundant intermixed mucous neck cells; upper 30% forming gastric pit; all cellular types comparatively small as compared to those of other bats examined. Depth of fundic mucosa 150 to 180.

Zymogenic cells typically pyramidal in form; nuclei spherical, small, and usually positioned in middle or lower half of cells, occasionally truly basal; basal portion of gland with chief cell complex rarely expanded into bulbous structure. Argentaffin cells not observed.

Parietal cells small with small, slightly ovoid, centrally located nuclei; slight variation in cell size apparent but variation mixed, not clinal; parietal cells occurring extremely rarely among zymogenic cells, equally uncommon within gastric pits of upper portion of tubule, little or no variation in distribution throughout fundic zone, relatively abundant in view of only moderate spatial distribution resulting from small size.

Mucous neck cells among parietal cells compressed horizontally with large similarly-shaped nuclei; cells extremely small, infrequent within parietal cell zone, never locally abundant within zone. Gastric pits moderate in depth, equal in breadth to remainder of gland, hence narrow, and with little or no apparent relative increase in depth within lateral arc of fundic caecum; pit cells markedly compressed laterally, large with extremely large disc-shaped nuclei heavily compressed laterally; cells increasing progressively in diameter from neck of pit to surface epithelium. Surface epithelium relatively shallow; nuclei large, rounded, and tapered toward base; mucous border narrow. Lamina propria mucosae typically scant basally and between glands.

Pylo-fundic transition.—Extensive breadth of transitional area attributable not only to pronounced invasion laterally of parietal cells into pylorus, but also to relatively abrupt diminution and loss of chief cells considerably proximal to pyloric sphincter (zone appearing expanded bidirectionally); glands essentially like adjacent fundic mucosa, differing in absence of chief cells and in that parietal cells distinctively more abundant along with numerous mucous neck cells in basal arc; more variation in depth of glands and slight increase in depth over that of fundus. Gradual increase in depth of gastric pits beginning just proximal to sulcus intermedius, zone of increase occupying approximately terminal third of transitional area, progres-

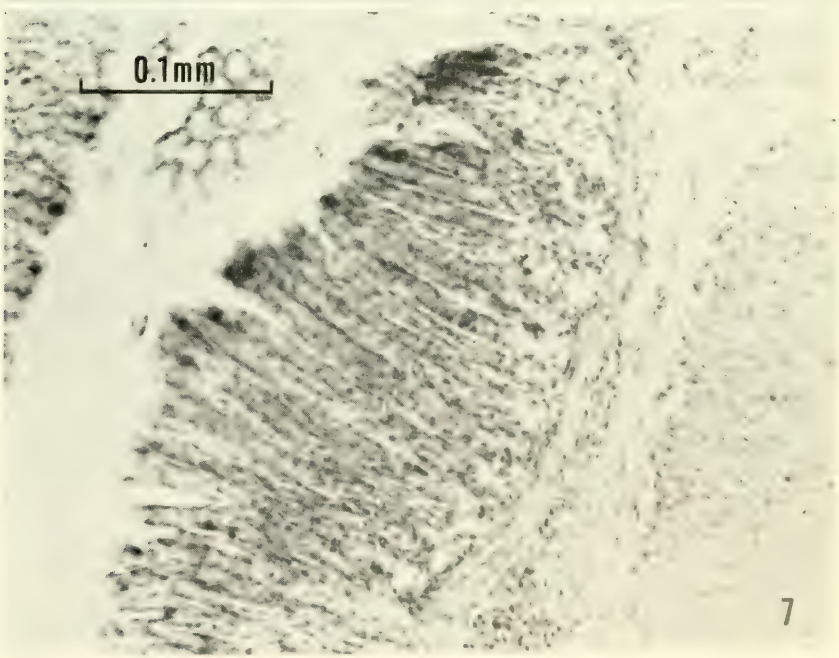


FIG. 6. Cardiac sphincter at gastroesophageal junction of *Noctilio labialis*. The fundic caecum is toward the left.

FIG. 7. Pyloric glands of *Noctilio labialis*.

sive increase corresponding to gradual loss of parietal cells within upper tubule; lamina propria equivalent to that of fundus. Depth 160 to 250.

Pyloric glands.—Terminal mucous-type glands (completely lack parietal cells) restricted to exceptionally narrow, symmetrical zone extending distally slightly beyond lip of sphincter into duodenal lumen; glands moderate and slightly variable in depth, slightly broader than fundic glands, remarkably uniform in cellular structure (usual single cell type present); cells consistent in morphology and diameter throughout tubule (Fig. 7), as well as pyloric zone, narrow with relatively large, circular, flattened nuclei (twice diameter of parietal nuclei); cells elongate and with moderately extensive mucous border; glands uniform in breadth excepting slight basal dilation, only slightly broader than fundic or transition glands. Lamina propria considerably more abundant basally, slightly more abundant between glands than within oxyntic type mucosa. Surface epithelial cells elongate and narrow compared to those of fundic glands. Depth of pyloric mucosa 160 to 200.

Glands of Brunner.—Restricted to single mass in immediate region of pyloric sphincter, relatively abundant; occupying entire distal surface of pyloric sphincter and proximal 1.0-1.5 mm of duodenum; thick layer of uniform depth, tapering little toward termination of distribution, ending aborally at lip of sphincter, not observed within pylorus of stomach; highly convoluted tubules of moderate and uniform breadth; cells long and narrow with extremely small, spherical, basally located nuclei (Fig. 8). Interposed smooth muscle fibers between tubules infrequent compared to other bats examined, except *Pteronotus parnellii;* lumen narrow throughout.

Remarks.—Noctilio labialis is unique among bats examined in the occurrence of an apparent anatomical cardiac sphincter at the gastroesophageal junction. Botha (1958a) examined the cardiac junctions of 13 species of distantly related mammals, describing that of "the bat" as a large, unbroken, conical papilla at the cardiac orifice, lined throughout with gastric mucosa, the edges of which form an extremely watertight "cork." This description is in marked contrast to the situation at the junction in *N. labialis,* although aptly describes cardiac junctions of most other species included in the present study. The squamous-lined flaps found in *N. labialis* also were observed macroscopically in one specimen of *Noctilio leporinus,* and must be considered unique to the family Noctilionidae among bats thus far described; additional investigations will be required to demonstrate that this structure is a physiologically efficient closure mechanism. The specialization at the cardiac junction of *N. labialis* may represent a distinct and independently evolved structure, unique among bats to the Noctilionidae and perhaps unique within the insectivore-primate-chiropteran line of mammalian evolution.

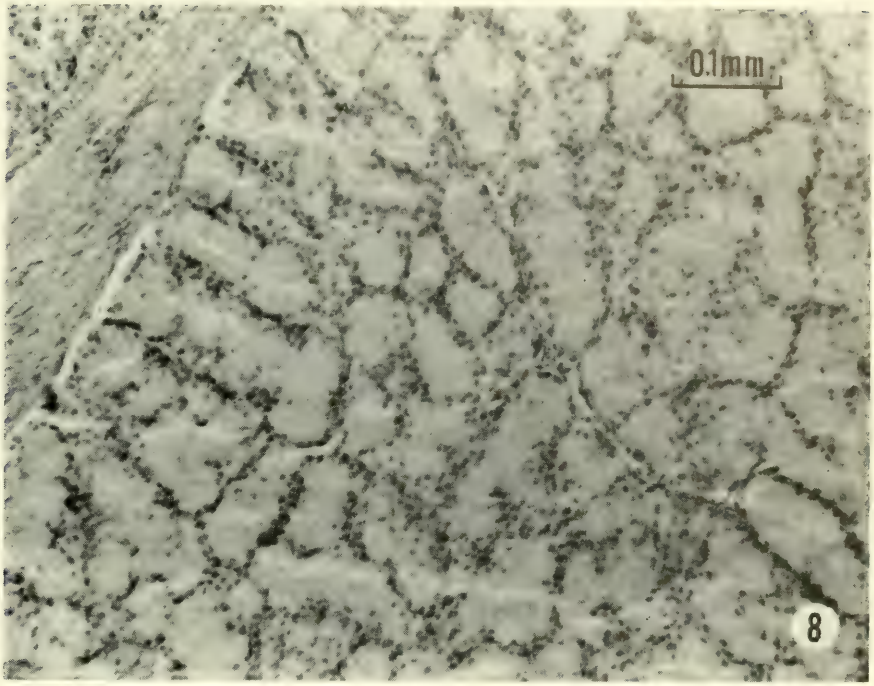


FIG. 8. Glands of Brunner of *Noctilio labialis*. Note the small nuclei.

Several unique features of the stomach of *N. labialis* are shared only with *Pteronotus parnellii*. The general outline of the stomach and great breadth of the pylorus at the sphincter are similar in these two species, as is the extensive pylo-fundic transition zone, with subsequent limiting of the pyloric glands to an extremely narrow region at the sphincter. Additional features common to *N. labialis* and *P. parnellii* include narrow oxynctic glands with comparatively small cellular elements, limited distribution of zymogenic cells within fundic tubules, and lack of distinctive reduction of the fundic mucosa within the caecum.

The stomach of *N. labialis* clearly follows the basic morphological pattern exhibited by other carnivorous bats examined, with notable specialization of the cardiac junction, perhaps a mechanism to aid in prevention of reversed passage of relatively large amounts of food into the abdominal esophagus.

Family PHYLLOSTOMATIDAE

Subfamily CHILONYCTERINAE

Pteronotus parnellii (Gray, 1843)

Specimens examined (1).—One specimen from Nicaragua of *Pteronotus parnellii fuscus* (KU 116992).

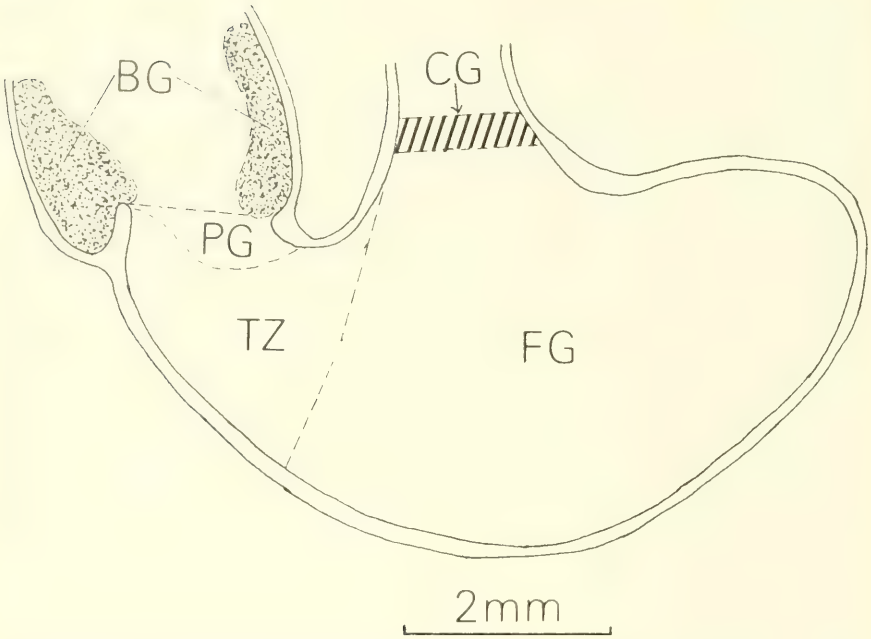


FIG. 9. Mid-longitudinal representation of the stomach of *Pteronotus parnellii*. For explanation of symbols, see Figure 3.

Overall dimensions.—Greatest length 8.6; greatest breadth 4.6; gastroesophageal junction to pyloric valve 2.4; gastroesophageal junction to apex of fundic caecum 4.0; breadth pylorus at sphincter 1.8.

General morphology.—Stomach tubular, short relative to breadth, highly symmetrical with gastroesophageal junction located approximately midway along lesser curvature (Fig. 9); upper and lower curvatures nearly parallel, but dorsolateral curvature pronounced (dorsal surface convex); fundic caecum short, directed slightly anteriorly with no evidence of dilation within dorsal surface, apex narrowly rounded; terminal portion of stomach extremely short and broad. Gastroesophageal junction and cardiac vestibule oriented nearly directly craniad, junction and cardiac orifice extremely broad; inferior border of stratified squamous epithelium only half depth of adjacent cardiac glands, gastroesophageal junction thus similar morphologically to that of *Natalus;* muscularis externa and muscularis mucosae continuous between esophagus and cardiac vestibule with no breaks or unusual orientation of fibers and no evidence of an anatomical cardiac sphincter; cardiac vestibule moderate in length, pattern of gradual coalition with lesser curvature similar to that in *Plecotus* (but vestibule shorter); incisura cardiaca absent (but slight thickening of circular muscle layer within wall that corresponds to zone of incisura cardiaca in other bats).

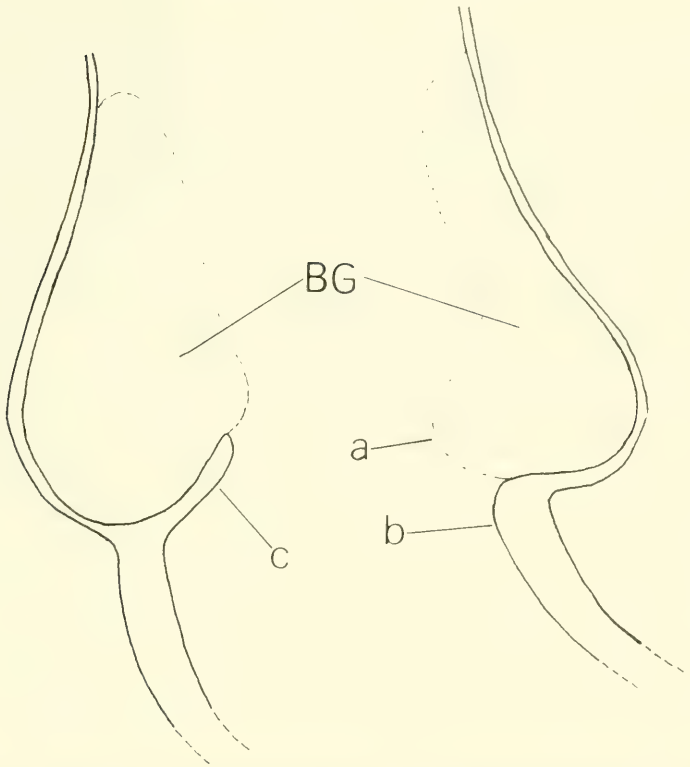


FIG. 10. Diagrammatic mid-longitudinal illustration of gastroduodenal junction of *Pteronotus parnellii*. **BG,** Brunner's glands; **a,** extension of Brunner's glands beyond lip of pyloric sphincter; **b,** pronounced reduction of pyloric sphincter (lesser curvature); **c,** small, narrow musculature of sphincter within greater curvature; anterior is toward the top in this figure.

Fundic caecum shallow; mucosa within caecum deep, muscular complement of caecal wall thick owing in large part to longitudinal muscle layer rather than circular layer. Stomach distal to cardiac vestibule directed antero-laterad, tapering gradually to extremely broad pyloric orifice. Musculature of pyloric sphincter poorly developed on greater curvature as an extremely narrow mass of circular muscle and muscularis mucosae extends outward and upward toward duodenal lumen (mass less in length than depth of glands of Brunner resting on its distal surface) (Fig. 10); sphincter of lesser curvature reduced to simple bulge in circular muscle layer; pyloric mucosa lining sphincter equivalent in depth to that of remainder of pylorus; pyloric orifice broad and displaced to left within tube; pyloric orifice inferior to esophageal junction *in situ*, although not pronounced because stomach nearly horizontal within body cavity. Lamina propria mucosae never abundant within stomach wall proper, moderately represented within rugae;

gastric mucosa comparatively deep among bats examined, occupying entire inner surface and never locally reduced (except extremely slight reduction within furrows of pylorus).

Musculature.—Muscular wall comparatively thick among bats examined and best developed among phyllostomatids studied; cardiac vestibule thick walled, musculature as deep as that of major portion of lesser curvature with circular layer principle component and longitudinal layer simple thin sheet. Wall of lesser curvature shallower than corresponding area of greater curvature only within terminal stomach, remaining portions (upper and lower walls of fundic caecum) approximately equal in depth, being slightly thicker than terminal half of lesser curvature; wall of greater curvature increasing progressively in depth from midpoint to pyloric sphincter, becoming two to three times breadth of comparable area within lesser arc through terminal 2 mm. Gathering of circular fibers into bundles prominent in lower wall of caecum, bundles becoming fewer in number and larger through upper wall to base of cardiac vestibule; pattern of depth of longitudinal layer similar to that observed in *Phyllostomus,* being exceptionally deep through lower and apical wall of caecum, decreasing through lower wall of terminal stomach, and extremely thin throughout lesser curvature; muscularis mucosae thin double sheet throughout wall, slightly deeper within rugae. Ganglia of Auerbach's plexus numerous except within cardiac vestibule and between vestibule and pyloric sphincter along lesser arc; lamina propria uniformly scant between muscularis mucosae and tunica muscularis throughout entire stomach wall, slightly more abundant beneath muscularis mucosae within rugae. Depth longitudinal layer 15 to 45, circular layer 30 (fundic caecum) to 180 (pylorus), muscularis mucosae less than 10 to 15 (within rugae).

Organization of gastric mucosa.—Rugal folds fewest in absolute number as well as least frequent per given area of gastric mucosa among bats examined; strictly directed longitudinally throughout entirety of dorsal and ventral surfaces of body of stomach from apex of fundic caecum to pyloric sphincter; isolated, transversely-oriented folds not observed anywhere within stomach lining, and folds not locally reducted in frequency; folds of cardiac vestibule continuous upward to gastroesophageal junction, although conforming to general longitudinal orientation (also the case in *Plecotus, Natalus, Noctilio,* and *Rhynchonycteris*). Depth of mucosa relatively uniform throughout except for cardiac glands; fundic mucosa slightly deeper than pyloric mucosa and slightly deeper in lesser curvature than in greater curvature, little reduced in fundic caecum; cardiac glands exceptionally deep in contrast to sharp decrease in depth of adjacent fundic mucosa; cardiac zone similar in depth, breadth, and morphology to that of *Phyllostomus.* Combined fundic glands and transitional zone occupying nearly

all of surface area as pyloric zone extremely short; fundic glands uniform in structure within zone and with no secondary regions of noteworthy variation from basic plan; transitional zone to pyloric mucosa broad in comparison to that of other phyllostomatids and occupies entire lesser curvature between gastroesophageal junction and pyloric mucosa (also extensive along greater arc); area of true pyloric mucosa relatively slight and asymmetrically distributed on upper and lower surfaces owing to extensive transitional zone and asymmetry of pyloric sphincter.

Cardiac glands.—Zone relatively narrow, equal in length throughout distribution; glands similar in morphology to those of *Phyllostomus* (long and narrow) although cellular components not identical; glands nearly uniform in breadth throughout, not prominently expanded at base; lumen extremely broad and uniform in breadth throughout; cells in lower third of tubule larger than those in upper portion, pyramidal, with large elongate nuclei compressed against basement membrane; cells in upper two-thirds of tubule extremely long and shallow with elongate, prominently compressed nuclei; mucous layer of lumen border shallow (in contrast to broad border of comparable cells in *Phyllostomus*). Lamina propria mucosae between glands better developed than within remainder of mucosa. Transitional area from cardiac to fundic mucosa twice breadth of cardiac zone; gastric pits in transitional zone decrease abruptly in depth, glands identical to cardiac mucosa except for presence of substantial number of scattered parietal cells; surface epithelium equivalent to that of remaining stomach (excepting slightly smaller nuclei). Depth of cardiac glands 350 to 390.

Fundus.—Fundic glands consistently narrow and highly convoluted, relatively long; fundic mucosa generally best developed in midportion of distribution, decreasing only slightly but progressively in depth in either direction laterally; all cellular types comparatively small in relation to other bats examined (except *Noctilio labialis*) by virtue of apparent uniform reduction in cytoplasmic mass of cells (because nuclei are universally large regardless of cell type); only slight variation in gland morphology within zone, variation entirely in number of zymogenic cells and depths of gastric pits. Cellular components more or less restricted to specific zones with slight alteration in lengths of zones within apical arc of fundic caecum; lower 15% restricted to zymogenic cells, middle 65% to parietal and mucous neck cells and upper 20% to gastric pits. Depth of mucosa 150 to 270 (cardiac vestibule).

Zymogenic cells never occupying more than basal 30% of gland; uniform in size, small and globular, not numerous, nuclei extremely large relative to cell size and always spherical with nuclei usually displaced laterally; zymogenic cells most abundant within glands of cardiac vestibule and through area directly posterior to greater curvature; argentaffin cells

extremely rare in bases of glands and less than one-half size of chief cells, rounded medially, tapering gradually toward periphery (outer limit of tubule), nucleus small and spherical.

Parietal cells, although within extensive spacial distribution, only moderately abundant owing to large numbers of interposed mucous neck cells; parietal cells normally elongate, ovoid, with extremely large, centrally located nuclei; clear cytoplasmic intercellular canals especially numerous; pronounced increase in cell size with corresponding decrease in nuclear size from bottom to top of distribution, uppermost cells extremely large; parietal cells never observed among basal zymogenic cells and reduced slightly in frequency within apex of fundic caecum as gastric pits are comparatively deeper.

Mucous neck cells uncommonly abundant among parietal cells as observed in *Phyllostomus,* increasing in numbers within gland from origin at chief-parietal cell boundary to surface epithelium and often observed in large clumps of 5 to 10 cells; mucous neck cells small, irregular in shape with large ovoid nuclei usually larger than those of adjacent parietal cells, nuclei remain large through gastric pits. Gastric pits shallow throughout most of fundic zone, increasing from usual 15% of thickness of tubule to 20-25% within furrows along apical arc of fundic caecum; neck cells of gastric pits with typically large nuclei previously described, nuclei decreasing in size only slightly to surface epithelium; mucous border deep throughout, lumen both shallow and narrow. Surface epithelium moderate in depth; nuclei extremely large, ovoid, not appreciably compressed laterally; lamina propria typically sparse basally, poorly developed between rather closely packed fundic glands.

Pylo-fundic transition zone.—Distribution of transitional glands to pyloric mucosa so extensive that true pyloric glands absent in portions of terminal pyloric tube; along lesser curvature transitional mucosa occupies all of area between inferior border of cardiac mucosa and initial increase in depth of musculature near sphincter (see Fig. 9), resulting in extremely broad zone; within greater curvature transitional glands extend through approximately one-third total length of stomach, essentially all of pyloric tube; glands identical in morphology along both curvatures up to terminal margin with pyloric glands where junction abrupt on lesser curvature (non-existent on greater curvature as true pyloric glands absent); glands essentially identical in structure to fundic glands (excepting absence of chief cells) with parietal and mucous cells extending to base; deepening of gastric pits abrupt at terminal margin of zone on lesser arc and gradual through greater curvature continuing to duodenal junction (parietal cells persisting within basal half of gland to duodenal junction); loss of zymogenic cells abrupt at initial margin; surface epithelium identical to that of fundus; depth equivalent to that of fundus; depth 210 to 250.

Pyloric glands.—Extremely limited distribution on lesser curvature; glands with parietal cells absent in greater arc and 50% broader than fundic or transitional glands; basal third of tubules broadly expanded with large cells containing ovoid nuclei moderate in size; cells of upper two-thirds of tubule small and more closely resembling mucous neck cells previously discussed, and with large, spherical nuclei; glands increasing gradually in breadth in upper half of tubule; basal two-thirds of lumen narrow, slightly broader in upper third; terminal glands along greater curvature generally fitting description given above although much narrower and containing mixed mucous and parietal cells (considered transitional glands in this account); intertubular and basal lamina propria as in fundic and transitional zones; depth 180 to 220.

Glands of Brunner.—Comparatively, best developed among phyllostomatids examined; always submucosal and occur throughout proximal 2.5 mm of duodenum; in single mass with no isolated lateral clumps; deepest along distal surface of pyloric valve, gradually decreasing in depth distally; not observed in stomach; typically highly convoluted and branched with tubules moderate in breadth; differing from other bats examined (excepting *Noctilio*) in having extremely small nuclei (always spherical) juxtaposed to basement membrane; cells numerous within cross-section of tubule, elongate and narrow; glands reduced slightly in breadth toward surface in comparison to basal region; pattern of exit into duodenal lumen as in other species.

Remarks.—Simplification of the stomach to a short, symmetrical, tubular crescent is characteristic of many obligate carnivorous bats as it is of *Pteronotus parnellii*. The presence of features observed in insectivorous bats in general is more apparent than in *Phyllostomus discolor*, another insect-feeding phyllostomatid. The tunica muscularis is best developed relative to stomach size, and the fundic caecum least distinctive, among the seven phyllostomatids examined. The terminal portion of the stomach is short and broad, totally unlike any other member of the family studied, although at least one side of the sphincter is long and narrow as in several other leaf-nosed bats.

General outline, topography, and orientation of orifices are somewhat similar to that observed in *Noctilio labialis* and *Plecotus townsendii*. The most unusual feature is the near loss of true pyloric mucosa at the terminal end, with extension of transitional glands laterally. This feature is in contrast to the relatively narrow transitional zone in most phyllostomatids. Orientation of mucosal folds is strictly longitudinal, a feature also unique among phyllostomatids studied.

Cellular elements of glandular types throughout the gastric mucosa lend distinctiveness to the stomach by consistently possessing uncommonly

large nuclei, in relation to the relatively slight cytoplasmic content of the cells.

Subfamily PHYLLOSTOMATINAE

Phyllostomus discolor Wagner, 1843

Specimens examined (3).—Three specimens from Nicaragua of *Phyllostomus discolor verrucosus* (KU 105952-53, 105958).

Overall dimensions.—Greatest length 12.1-12.4; greatest breadth 5.0-5.2; gastroesophageal junction to pyloric valve 3.5-3.6; gastroesophageal junction to apex of fundic caecum 4.1-4.4; breadth of pylorus at sphincter 1.9-2.0.

General morphology.—Stomach reniform, long and generally symmetrical; greater and lesser curvatures nearly parallel; marked curvature in frontal plane with less marked dorsolateral curvature (dorsal surface convex) from gastroesophageal junction to apex of fundic caecum; fundic caecum long and slightly dilated at apex on dorsal surface; terminal stomach long but pyloric endpiece abruptly tapered and relatively short. Cardiac vestibule extremely short and tubular, junction with lesser curvature abrupt (extends only about 1 mm superior to lesser curvature); uniform in diameter, not tapered, breadth equivalent to that of esophagus; enters body of stomach perpendicularly beneath sharply-angled esophagus; thick-walled as most of remaining stomach in that musculature well developed. Gastroesophageal junction abrupt; circular and longitudinal layers continuous at junction, muscularis mucosae permeated by strands of collagenous tissue although most muscle fibers continuous. Incisura cardiaca present, although extremely shallow and arises as a result of anterior expansion of the fundic caecum, with slight depression resulting at junction of lesser curvature and cardiac vestibule; circular muscle layer markedly thickened at incisura with compartmentalization of fibers into radiating sheets but no conclusive evidence of anatomical cardiac sphincter. Fundic caecum relatively long and tubular, directed antero-laterally; dilated at apex and hooking slightly dorsally; apex narrowly rounded; caecum not appearing as a distinctive chamber but rather as a tubular extension as observed in *Plecotus* and *Molossus*. Tubular stomach distal to gastroesophageal junction extensive, although broader and less extensively recurved than other phyllostomatids examined (excepting *Pteronotus*); decreases gradually in breadth to pronounced constriction (sulcus angularis) approximately 2.5 mm below pyloric sphincter (Fig. 11); terminal endpiece to sphincter narrow; gastroesophageal junction superior to pyloric sphincter in stomach *in situ*. Pyloric sphincter greater in length and breadth on greater curvature and expanded along lumenal rim to form narrow lip at orifice; circular layer and muscularis mucosae form contributing muscle layers; external constriction at sphincter slight. Musculature thick with all muscle components well repre-

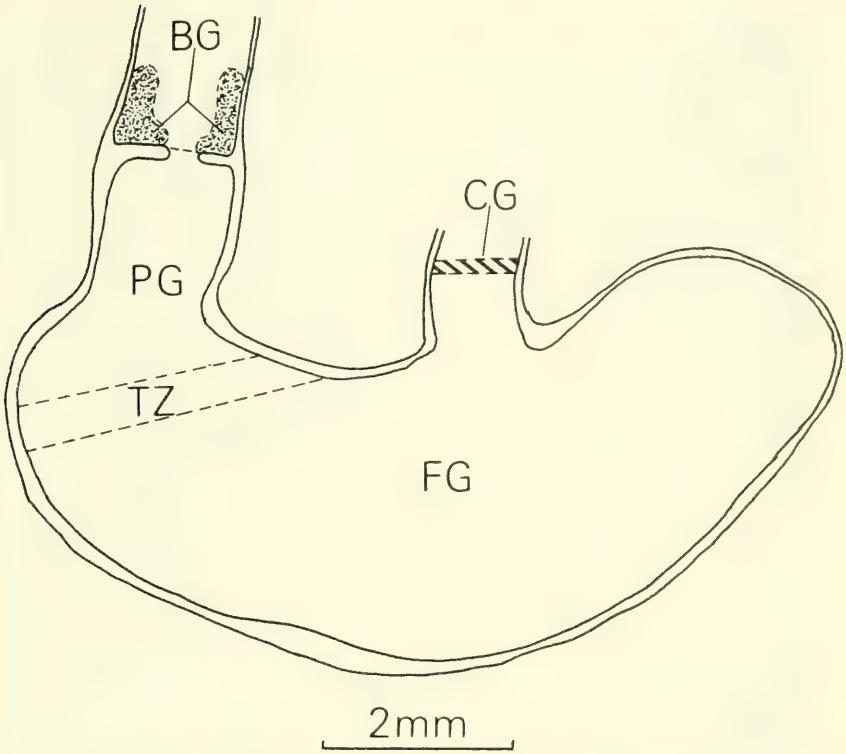


FIG. 11. Mid-longitudinal representation of the stomach of *Phyllostomus discolor*. For explanation of symbols, see Figure 3.

sented (including muscularis mucosae) and little reduction anywhere except in terminal arc of fundic caecum.

Rugal folds relatively few in number; gastric mucosa thick throughout, reduced in depth only within furrows of fundic caecum, mucosa deepest within fundus of lesser curvature in pylorus. Lamina propria best developed of all bats examined, particularly within pyloric region and immediately adjacent fundic mucosa between muscularis mucosae and circular layer, although typically narrow sheets within wall of fundic caecum. Stomach generally similar in gross morphology to those of other carnivorous species examined.

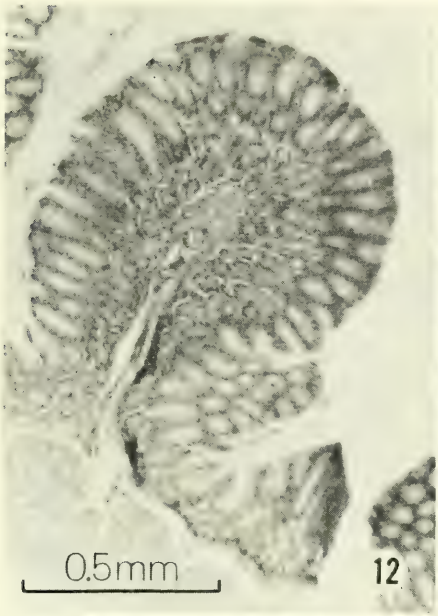
Musculature.—Both external layers exceptionally deep throughout (excepting major portion of fundic caecum); circular layer substantially deeper than longitudinal except in terminal two-thirds of fundic caecum; musculature between gastroesophageal junction and lesser curvature moderate in depth in comparison to most of remaining stomach, notably deeper than musculature of adjacent esophagus and somewhat thickened at junction with lesser curvature.

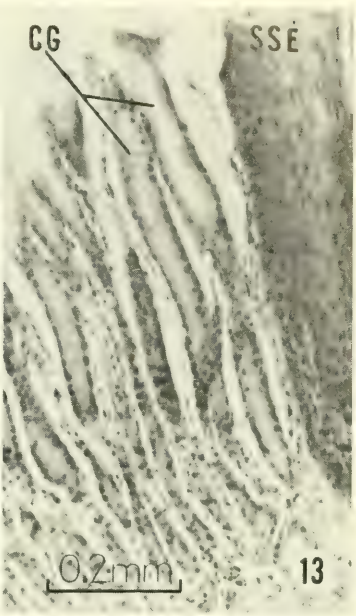
Longitudinal layer deep in comparison to other phyllostomatids examined; moderate in depth through greater arc of pyloric tube, becoming deeper through greater curvature, but decreasing slightly within apex of caecum; reduced to extremely thin sheet in upper surface of caecum and moderate in depth throughout remainder of lesser curvature.

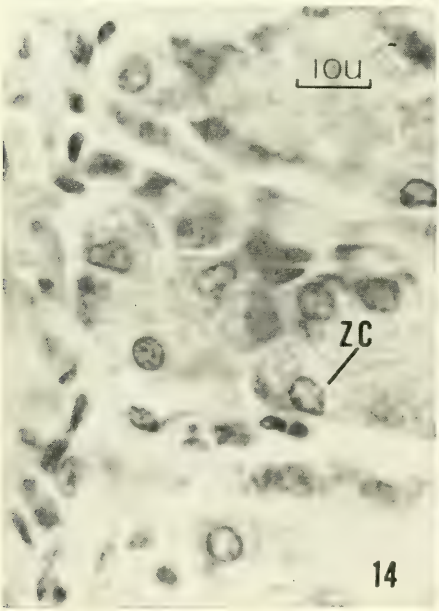
Circular layer deep throughout stomach wall (except for apex and upper wall of caecum where equivalent in depth to longitudinal layer); generally deeper throughout greater than lesser curvature; especially pronounced local thickening midway along greater curvature of tubular stomach, slight local thickening at bases of rugae; circular layer extensively gathered into large bundles surrounded by speta and permeated centrally with moderate amounts of loose lamina propria originating from normally thin interlayer connective tissue sheet; distribution of bundles from midpoint of greater curvature to most lateral extremity of fundic caecum.

Muscularis mucosae uncommonly thick throughout and double-layered; substantially thickened in rugal folds as compared to stomach wall proper; continuous with muscularis mucosae of esophagus at junction in absence of anatomical cardiac sphincter. Connective tissue between circular muscle and muscularis mucosae best developed as a continuous layer among bats examined; especially pronounced within tubular stomach, but occurring as relatively deep region throughout stomach (excluding apex of fundic caecum), connective tissue especially well represented within rugal folds; collagenous fibers most abundant within rugae, unusually abundant within muscularis mucosae but less well represented in outer wall; ganglia of Auerbach's plexus abundant. Depth longitudinal layer 15 to 45, circular layer 30 (caecum) to 220 (pylorus), muscularis mucosae 15 to 25.

Organization of gastric mucosa.—Mucosa gathered longitudinally into deep, broad rugae throughout all of stomach except along midline of greater curvature within non-tubular area, in which rugae are short, discontinuous projections that are directed antero-posteriorly (Fig. 12); slight "zig-zag" orientation of folds within entire non-pyloric stomach, although uniformly parallel and never truly interdigitating. Folds relatively few in number and reduced locally in frequency within apical arc of fundic caecum; folds well developed within short cardiac vestibule, although relatively few in number owing to narrowness of tube. Gastric mucosa comparatively deep throughout stomach; cardiac glands unusually long; fundic mucosa deepest within cardiac vestibule and relatively deep throughout entire distribution, also being thick along sides of rugae but slightly shallower at apexes of folds and consistently reduced in furrows between folds; average depth of fundic glands at apex of caecum slightly less than in remaining fundic zone but deeper within lesser curvature compared to greater curvature; pyloric mucosa slightly deeper than fundic and somewhat more variable







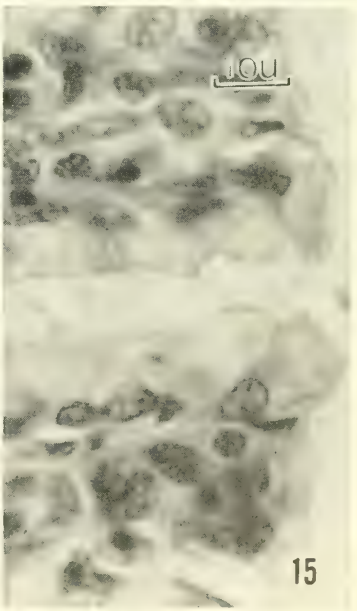


FIG. 12. A small, isolated, superiorly directed fold of gastric mucosa within the greater curvature of *Phyllostomus discolor*.

FIG. 13. Cardiac glands (**CG**) of *Phyllostomus discolor* and gastroesophageal junction, showing stratified squamous epithelium (**SSE**).

FIG. 14. Zymogenic (chief) cells (**ZC**) at base of a fundic gland in *Phyllostomus discolor*.

FIG. 15. Gastric pit of fundic gland (*Phyllostomus discolor*). Note the broad lumen and deep mucous border.

in depth. All basic glandular types present; cardiac zone extremely narrow (only 0.1 mm at gastroesophageal junction); true fundic mucosa occupies all of caecal stomach, much of tubular stomach on greater curvature, with less extensive distribution along lesser curvature resulting in correspondingly greater representation of pyloric glands along the lesser arc; transition zone to pylorus narrow, occupying brief zone just proximal to pyloric constriction, equal in length on upper and lower surfaces; pyloric mucosa extensive, asymmetrically distributed, occurring throughout short, terminal section down through pyloric constriction to abrupt junction with pylo-fundic transition zone and cranially to distal surface of pyloric sphincter with no invasion into duodenal lumen.

Cardiac glands.—Extremely thin and relatively straight tubular glands (Fig. 13) expanded only slightly at base; gradually increasing in breadth within upper half; occupying zone only two to three glands in breadth at gastroesophageal junction; single cell type present; cells small, long and narrow, with small, laterally compressed nuclei in upper half (Fig. 13) and more rounded nuclei in lower half; mucous border narrow; lumen also narrow; transitional area to fundus as narrow as cardiac zone and the equivalent of three glands in breadth; surface epithelium deep, cells with large nuclei that are markedly compressed; depth of mucosa 420 to 460.

Fundus.—Glands extensively variable within stomach, both in depth and in representation of particular cell types. Zymogenic cells in heaviest concentration within midregion of fundic mucosa, decreasing slightly in number in either direction laterally; parietal cells also most abundant within midregion, decreasing substantially to apex of caecum and increasing in direction of pylorus as zymogenic cells decrease; decrease in parietal cells in caecum owing to substantial increase in depth of gastric pits throughout entire fundic mucosa within fundic caecum, although overall decrease of glandular depth slight. Gastric glands relatively short in relation to large size of stomach, broad (excepting those of cardiac vestibule and lesser curvature immediately surrounding cardiac vestibule). Cell types generally restricted to specific zones within gland throughout most of fundic mucosa (except mucous neck cells, which occur throughout where zymogenic cells absent); lower 40% of fundus composed of zymogenic cells with occasional scattered parietal cells, middle 30% with parietal cells and frequent mucous neck cells, upper 30% represents gastric pits. Depth of mucosa 250 throughout most of fundus to 150 within caecum.

Zymogenic cells (Fig. 14) abundant throughout fundic zone; large, irregularly shaped, and of moderate size; nuclei spherical and always laterally displaced; cells sometimes polyhedral or ovoid but more regularly triangular; lumen narrow through zone of chief cells; base of gland with chief cells, although extremely narrow, slightly expanded into bulb. Argentaffin cells

most abundant within complex of chief cells of any bat examined; extremely small in comparison to adjacent chief cells; more or less rectangular with large spherical nuclei; outer cytoplasm filled with fine argentaffin granules that stain pink with standard haematoxylin and eosin procedure; cells confined to lower apical arc of chief cell distribution.

Parietal cells moderate and comparatively uniform in size in relation to those of other phyllostomatids examined; most abundant within narrow midregion, less abundant as scattered elements among uppermost chief cells; usually rounded, rarely ovoid; nucleus always ovoid and moderate in size, centrally located within cell; parietal cells may be relatively few due to large number of mucous neck cells within midregion of gland.

Mucous neck cells small, having large, round, peripheral nuclei; mucous border deep, much as in *Pteronotus;* unique among phyllostomatids examined in being more abundant in area of parietal cells than parietal cells themselves. Gastric pits extremely deep, deepest of any phyllostomatid observed, occupying upper 30% through most of fundus to 80% in glands at apex of fundic caecum where parietal cells all but absent. Neck cells extremely large; mucous border deepest of any bat examined (Fig. 15); nuclei large and ovoid in lower half of layer, prominently compressed in upper half; lumen a broad chamber increasing only slightly in breadth to surface. Surface epithelium deep; cells with extremely large rounded nuclei. Lamina propria typically sparse beneath glands.

Fundo-pyloric transition.—Zone narrow (see Fig. 11), approximately equal in length on both curvatures; loss of parietal cells gradual with few cells persisting into basal area of proximal-most pyloric glands; persisting parietal cells extremely small; loss of zymogenic cells much more abrupt; deepening of gastric pits gradual with progressive loss of parietal and chief cells; area of transition in which parietal cells extend to base of gland extremely narrow; depth 250 to 310.

Pyloric glands.—Pyloric glands extensive and reflect generally well-developed mucous cell system in *Phyllostomus;* glands variable in depth, local thickenings represent deepest portions of gastric mucosa with glands prominently deeper through greater in contrast to lesser curvature; glands long and extremely broad (Fig. 16); composed of single cell type (cells small with large nuclei in basal half of gland), increasing substantially within upper half and becoming giant columnar type with relatively small, progressively more ovoid nuclei; lumen extremely broad, hence glands uncommonly large; origin of pyloric glands at terminus of fundic mucosa fairly abrupt, extending laterally to distal edge of pyloric sphincter; lamina propria beneath glands reduced as in remainder of mucosa; pyloric zone especially well developed in length and depth in *Phyllostomus* as compared to other phyllostomatids examined; depth of mucosa 200 to 310.

FIG. 16. Pyloric mucosa of *Phyllostomus discolor*.

Glands of Brunner.—Glands well developed at pyloric sphincter and as moderately deep layer through proximal 3 mm of duodenum; always submucosal, never occur within stomach mucosa; distribution along distal surface of sphincter only slightly deeper than that within submucosa of duodenal wall (former region markedly deepened layer in all other bats examined having large complement of Brunner's glands); glands occur as single mass in duodenum with isolated patches not observed; glands virtually identical in cross-sectional morphology to those of *Pteronotus;* orifices between crypts of Lieberkühn; lumen relatively broad.

Remarks.—The stomach of *Phyllostomus discolor* exhibits a mosaic of characters of which some are common to other phyllostomatids and others are common to carnivorous species irrespective of systematic affiliation. The tubular nature of the stomach is consistent with findings for obligate insect feeders, and suggests at least a gross morphological adaptation to a diet rich in proteinaceous foods. Recent studies (Arata *et al.*, 1967) have alluded to the strongly insectivorous feeding habits of *Phyllostomus discolor* and *P. hastatus*, species belonging to a family predominantly composed of fruit and nectar feeders.

Other features observed in *Phyllostomus* include a more or less tubular fundic caecum with only a slight dorsolateral dilation at the apex, short

tubular cardiac vestibule, well-developed musculature, and lack of pronounced cranial recurvature of the pylorus.

Although clearly showing features normally observed in carnivores, *P. discolor* retains conditions common to most other phyllostomatids. These include a narrow relatively abrupt pylo-fundic transition zone, dilated fundic caecum (although only slightly on dorsal wall), an elongate terminal stomach, and a relatively thin muscular complement within the pyloric sphincter.

Mucous production must be extensive owing to the marked development of pyloric glands and notably deepened gastric pits of the fundic glands, as well as numerous mucous neck cells within the middle portion of the fundic glands.

Subfamily Glossophaginae

Glossophaga soricina (Pallas, 1766)

Specimens examined (2).—Two specimens from Nicaragua of *Glossophaga soricina leachii* (KU 105984, 105993).

Overall dimensions.—Greatest length 12.0-13.5; greatest breadth 4.7-4.9; greatest length fundic pouch 4.3-4.5; greatest breadth fundic pouch 3.7; gastroesophageal junction to pyloric sphincter 4.8-5.3; gastroesophageal junction to apex of fundic caecum 5.0-5.2; breadth pylorus at sphincter 1.7.

General structure.—Large, saccular, bean-shaped, with extensive development of fundic caecum; both saccular and terminal parts well developed (Fig. 17); marked curvature of stomach in two planes—pronounced curvature in frontal plane and less pronounced curvature in transverse plane (planar orientation of organ *in situ*). Fundic caecum extensively developed (Fig. 18) and set off by sulcus on dorsal surface; pronounced invagination of muscularis externa on greater and lesser curvatures resulting in distinctive "pouch" and semi-ruminate condition; caecum dilated on dorsal side, hence caecum spacious; apex blunt; sulcus delimiting fundic "pouch" at incisura cardiaca on lesser curvature extending posteriad to midway along greater curvature between apex of fundic caecum and pyloric bend (see Fig. 17). Region of stomach distal to gastroesophageal junction tapering gradually to midway between cardiac and pyloric junctions (where pronounced crook in tubular stomach occurs, with terminal part recurved craniad and terminal end-piece then approximately parallel to esophagus); sulcus intermedius present but poorly developed, stomach narrows abruptly just distal to "bend" and remains uniformly narrow to pyloric sphincter.

Incisura cardiaca pronounced and accompanied by noteworthy local thickening of muscularis externa; thickened muscle mass dense and partially compartmentalized into thin sheets radiating from incisura; sheets separated by thin fibrous septa similar to those described by Dearden (1966) in microtine rodents; cardiac orifice relatively narrow. Cardiac vestibule extremely

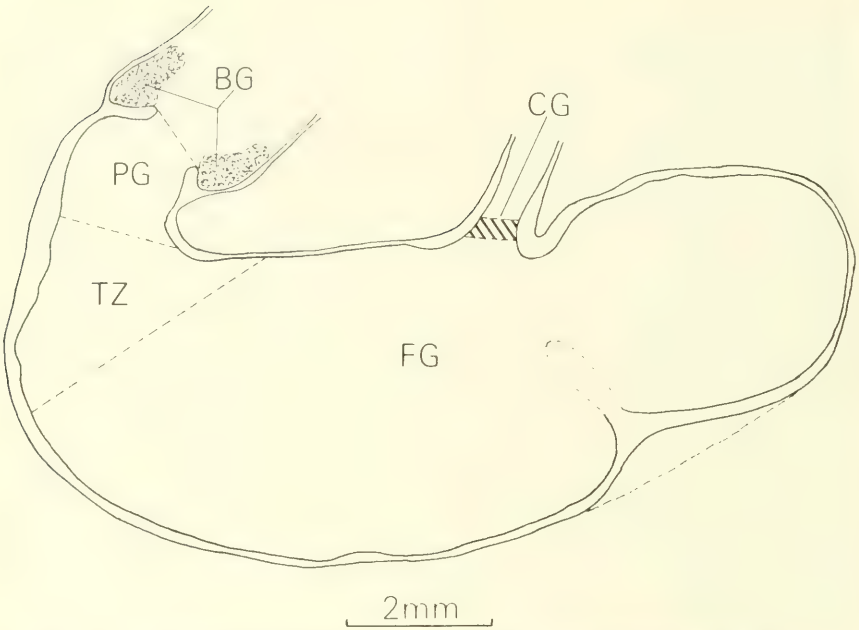


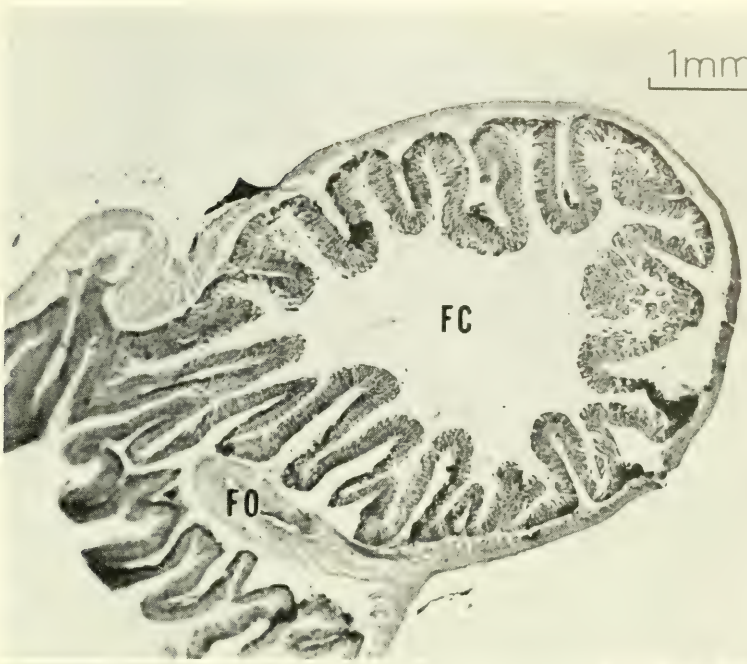
FIG. 17. Mid-longitudinal representation of the stomach of *Glossophaga soricina*. For explanation of symbols, see Figure 3.

short and with no reduction of included gastric mucosa; longer on pyloric than caecal side owing to angular entry of esophagus into stomach.

Pyloric sphincter asymmetrical (Fig. 19); musculature of pyloric sphincter substantially more massive on greater than on lesser curvature, muscle mass generally thinnest at junction with stomach wall, increasing gradually in breadth and terminating at rounded apex on luminal surface; muscle of sphincter on greater curvature several times more massive than on lesser curvature; relatively shallow; gastric mucosa (pyloric glands) covering pyloric sphincter; glands of Brunner completely covering distal edge of sphincter muscle mass; only circular and muscularis mucosae layers contribute to pyloric sphincter. Gastric mucosa lines entire surface of stomach, little reduced anywhere; stomach semi-compartmentalized, possibly adapted for storage of food material, presumably to extend length of time during which food is exposed to gastric digestion .

Musculature.—Extensive variation in depth of component muscle layers within stomach; outer longitudinal layer always considerably thinner than inner circular layer; circular layer thickened at incisura cardiaca and somewhat compartmentalized into sheets of fibers by thin fibrous septa (restricted to incisura cardiaca proper).

Outer longitudinal layer extensively dilated throughout lesser and greater



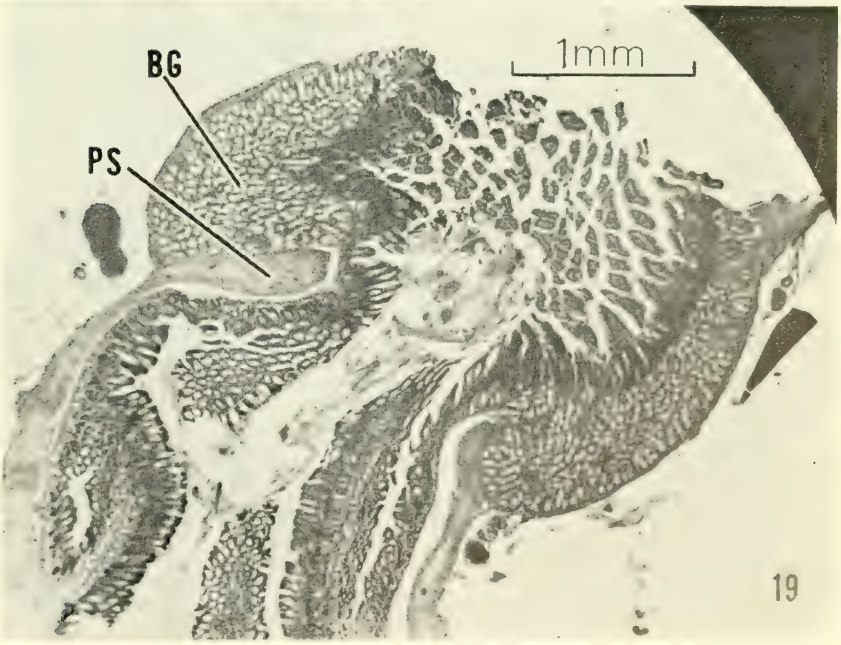


FIG. 18. Longitudinal section of the fundic caecum (within dorsal half) of *Glossophaga soricina* showing fold in body wall (**FO**) and fundic caecum (**FC**).

FIG. 19. Pyloric sphincter of *Glossophaga soricina*. Note the asymmetry of the sphincter musculature, showing Brunner's glands (**BG**) and pyloric sphincter (**PS**).

curvatures of fundic stomach distal to cardiac junction; remaining fundus (fundic caecum) with relatively thickened longitudinal layer on superior and inferior surfaces, whereas circular layer in these two areas only slightly thicker than longitudinal muscle and clumped into many fibrous bundles along inferior surface; both layers notably dilated in apex of caecum, occurring there as extremely thin sheets. Pyloric tube musculature extensively thickened on greater curvature (both longitudinal and circular layers) (Fig. 19), narrowing again to a thin remnant just inferior to pyloric valve; musculature of lesser curvature of pyloric tube less than one-third breadth of corresponding tissue of greater surface at its maximum.

Muscularis mucosae narrow; filamentous sheets throughout stomach, most prominent in pyloric tube. Depth of longitudinal layer 10 to 45, circular layer 30 to 140, muscularis mucosae 7.

Organization of gastric mucosa.—Mucosa gathered longitudinally into parallel rows throughout all of pyloric area and tubular fundus up to and including cardiac vestibule; folds of saccular fundic caecum oriented longitudinally on sides (dorsal and ventral surfaces *in situ*) and radially on upper and lower surfaces, as well as apex of caecum and effacing one another in spoke-like fashion within caecum; folds broad and deep in tubular stomach and reduced somewhat in breadth (although not in frequency) in caecum due to general reduction in depth of mucosa in this region; folds in mid-longitudinal plane rarely broadly expanded at apex in contrast to those of *Plecotus;* mucosa only slightly deeper at apex of rugae than at bases and sides of furrows between rugae; fundic mucosa slightly deeper on lesser than greater curvature, reduced in caecum and extreme oral portion of cardiac vestibule; pyloric mucosa deep in proximal area of pyloric zone, reduced substantially in depth at orifices and along pyloric sphincter.

All basic glandular areas represented; cardiac zone relatively broad with transition to fundus abrupt; pyloric glands occupy all of pyloric endpiece (that portion distal to point of narrowing); transition from fundus to pylorus narrow on lesser curvature, twice as broad on greater curvature, loss of basal zymogenic cells gradual with deepening of gastric pits and establishment of mucous complement of pyloric glands relatively abrupt; all of fundic caecum and non-pyloric stomach occupied by fundic type glandular mucosa (see Fig. 17 for map of glandular areas).

Cardiac glands.—Band moderate in breadth (1 mm), extending approximately to base of muscular fold of incisura; glands relatively numerous in comparison to most other bats examined; demonstrable transition to fundic mucosa present, although transition relatively abrupt and characterized by scattered parietal cells in basal half of gland; cardiac glands extremely short and broad (Fig. 20), of fairly uniform height throughout zone and with broad lumens; basal cells small, compact, upper cells larger and

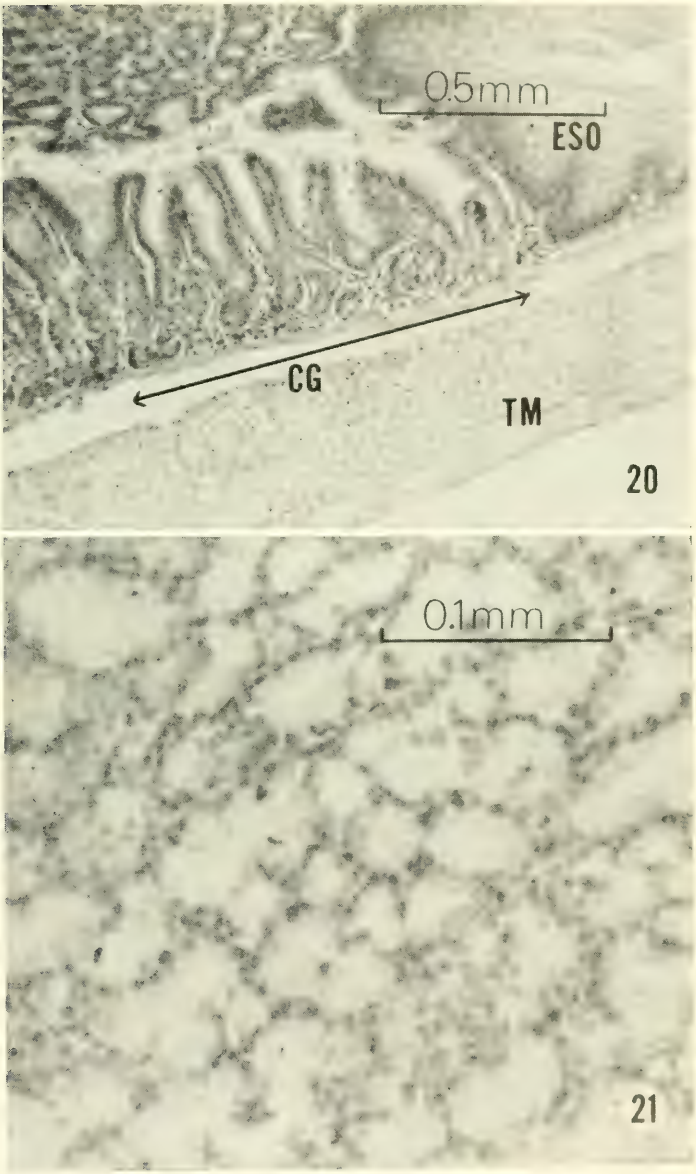


FIG. 20. Zone of cardiac glands at the gastroesophageal junction of *Glossophaga soricina*, showing cardiac glands (**CG**), esophagus (**ESO**), and tunica muscularis (**TM**).

FIG. 21. Brunner's glands in the duodenum of *Glossophaga soricina*.

usually with large circular nuclei; gastric pits of cardiac glands broad, increasing greatly in breadth toward mucosal surface where breadth so great as to lend villi-like appearance to glands (Fig. 20); loose lamina propria extensive between slightly bulbular bases of glands, less extensive with onset of fundic mucosa; abrupt transition aborally from stratified squamous epithelium of esophagus; depth of mucosa 125.

Fundus.—Variation in morphology within stomach due to reduction in numbers or loss of certain cell types in specific regions; mucosa within and adjacent to fundic caecum slightly shallower than that of remaining fundus and gastric pits broader, "stunted" condition of glands in caecum due to reduction in number of all three cell components (zymogenic, parietal, mucous neck); gastric pits deep in fundic caecum, narrow and shallow in remainder of fundus; lamina propria restricted mostly to narrow belt beneath bases of glands. Depth of fundic mucosa 140 to 180 in fundic caecum and 170 to 220 in tubular portion of fundus.

Zymogenic cells usually occupy lower third of gland and occasionally basal half in midregion of fundus near gastroesophageal junction, reduced or absent only in extreme apex of fundic caecum; rectangular to polyhedral with large, spherical, peripherally-displaced nuclei; granulation pronounced in specimens examined; parietal cells rarely observed within zymogenic cell complex.

Parietal cells normally in middle third of gland; extremely large, often four times breadth of adjacent mucous neck cells and circular to slightly ovoid; nuclei large (breadth equals one-third breadth of cell) and circular; distinct and marked increase in size of cells from bottom to top of gland (cells vary in diameter from 7 microns at base to 18 in upper gland); basal cells irregular in shape due to more compact cellular elements than within upper portions.

Mucous neck cells confined to upper two-thirds of tubule, continuing into gastric pits (as in all other bats examined) from origin among parietal cells; cuboidal or trapezoidal with large spherical nuclei (nearly twice as large as those of parietal cells); extending to base of glands in fundic caecum along with parietal cells (replace zymogenic cells). Argentaffin cells extremely rare, found mostly among zymogenic cells in basal arc.

Gastric pits of fundic glands distal to caecum shallow, those within caecum deeper, broader, 30-60% length of glands; surface epithelial cells short and with elongate, laterally-compressed nuclei, decrease markedly in size from luminal surface to bottom of gastric pit; mucous border of epithelium not extensive.

Pylo-fundic transition.—Extremely narrow zone on lesser curvature, more extensive on greater arc, occupies approximate region of pyloric bend; depletion of chief cells gradual; broad area with absence of chief cells yet

with shallow gastric pits; gastric pits deepen abruptly in terminal portion of zone; parietal cells numerous and extend into base of glands, relatively small throughout glands; depth 200.

Pyloric glands.—Occupy tubular portion of stomach approximately distal to pyloric bend and up to superior surface of pyloric sphincter; glands as deep or slightly deeper than those of fundus, although notably broader and with substantially thicker, more compact surface epithelium; composed of single cell type (with exception of occasional basal argentaffin cell); basal mucous cells extremely compact, base of gland bulbular; nuclei large, spherical; from midregion upward cells increase in size, nuclei enlarge and become progressively more laterally flattened and "club-shaped"; lamina propria more extensive than in fundic mucosa, areolar connective tissue prominent beneath glands; gastric pits broad and lumen of gland extremely broad with two glands opening into single pit; pyloric glands well developed, extensively distributed when compared to many other bats examined; depth of pyloric glands 150 to 250.

Glands of Brunner.—Limited to proximal-most 2 mm of duodenum and never found superior to muscularis mucosae except in limited area at apex of pyloric valve; narrow tubules highly coiled with broad lumen; cells irregularly shaped with large, spherical, peripheral nuclei (Fig. 21); smooth muscle fibers and lamina propria observed only rarely between glands.

Remarks.—The stomach of *Glossophaga soricina* is most distinctive in the presence of a rounded, spacious fundic caecum prominently dilated on the dorsal surface, and unique among bats examined with the presence of a distinct sulcus deliminating the fundic pouch from the remaining stomach. A figure depicting the gastrointestinal tract of *Glossophaga* included in accounts of gross morphology of several bat stomachs by Park and Hall (1951) illustrates the dilated portion of the caecum, and corresponds well with my findings. The stomach cannot be considered truly ruminate, as no rigid partition exists, although the stomach clearly approaches a two-chamber condition (Fig. 17).

Rouk (1968) described and illustrated the stomach of *Leptonycteris sanborni*, a North American nectivore of the subfamily Glossophaginae. The stomach of this species agrees well (as illustrated by Rouk) with that of *G. soricina* in general shape and configuration of gross features, particularly in orientation and morphology of the terminal stomach, including the pyloric sphincter. Also, the orientation and location of the gastroesophageal junction as reported by Rouk is virtually identical to that of *Glossophaga*, although the vestibule is somewhat more extensive in *L. sanborni*. Rouk states that the stomach of *L. sanborni* is "more globular or saccular" than those of the insectivorous types he examined, although an included mid-

longitudinal drawing does not conclusively illustrate this point. Rouk also noted that the pyloric sphincter was thinner than that of insectivorous types examined, a feature observed in *Glossophaga* and several other phyllostomatids I have examined. Rouk's map of the distribution of glandular types shows the glands of Brunner to be extremely restricted in distribution, unlike the rather large mass at the pyloric sphincter of *Glossophaga.* The relative depths of the tunica muscularis are similar in the two species, although transverse gathering of circular fibers into bundles extends craniad more in the fundic caecum of *Glossophaga.*

The gastric mucosa of *G. soricina* is unique among herbivorous phyllostomatids examined in being rather generalized, composed of relatively short, broad glands somewhat resembling those of *Plecotus;* the three cellular components each are more or less confined to one-third the length of the tubule and overlap little in distribution.

Rouk's description of the mucosal folds of *Leptonycteris sanborni* suggests existence of some degree of anastomosing, as observed in the fundic caecum of *Glossophaga,* although the description is unclear as to the exact location of anastomosing folds, and difficult to interpret comparatively. He also reported the presence of what appeared to be clumps of cells identical to glands of Brunner within the pylorus. No glands positively identified as Brunner's (histologically or histochemically) were observed in the stomach of *Glossophaga.*

Subfamily CAROLLINAE

Carollia perspicillata (Linneus, 1758)

Specimens examined (2).—Two specimens from Nicaragua of *Carollia perspicillata azteca* (KU 106036, 106064).

Overall dimensions.—Greatest length 10.1-11.4; greatest breadth 5.0-5.5; gastroesophageal junction to apex of fundic caecum 4.0-4.7; gastroesophageal junction to pyloric sphincter 4.1-6.2; breadth of fundic caecum 4.0-4.1; breadth pylorus at sphincter 3.9.

General structure.—Stomach club-shaped and decidedly asymmetrical with moderately well-developed cardiac vestibule (Fig. 22); tubular stomach markedly elongate; marked dorsolateral flexure affecting entire stomach, dorsal surface concave; stomach most closely resembling that of *Glossophaga* among bats examined in general stomach outline; gastroesophageal junction abrupt, muscularis externa continuous with muscularis of esophagus, muscularis mucosae thickened slightly although in continuous sheets; no anatomical cardiac sphincter. Cardiac vestibule moderately developed (Fig. 23), entering stomach at pronounced angle to lesser curvature creating marked incisura cardiaca; expanding gradually from origin at gastroesophageal junction and disappearing gradually within lesser curvature; extremely thin-walled compared to remaining areas of stomach although mucosal

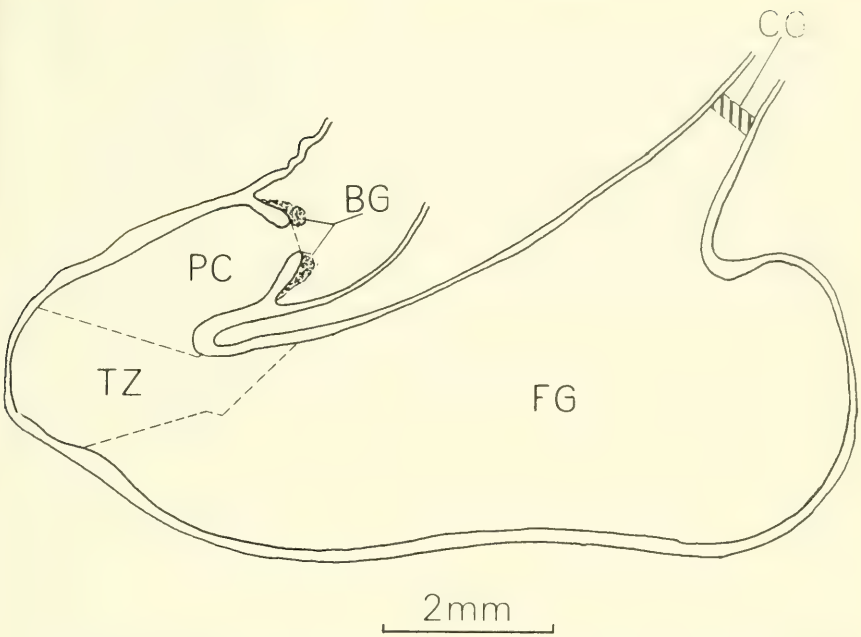


Fig. 22. Mid-longitudinal representation of the stomach of *Carollia perspicillata*. For explanation of symbols, see Figure 3.

membrane deep within vestibule; incisura cardiaca relatively broad and deep (with thickening of circular muscle layer only, no comparable condition in other musculature); incisura best expressed within dorsal half of stomach as dilated dorsal wall of fundic caecum tends to expand somewhat craniad.

Fundic caecum saccular, appearing as dilated circular bulb lateral to vestibule (Fig. 24), heavily dilated and rounded on dorsal (back) surface, comparatively small and less distinctive as "chamber" than caecum of *Glossophaga;* caecum distinctive not only externally but by pattern of mucosal gathering within, never truly separated anatomically by folds of musculature or gastric mucosa; musculature of caecum not reduced appreciably in depth but muscle layers loosely organized with unusually heavy complements of elastic fibers within muscularis; complex, oblique orientation of longitudinal layer throughout caecum, extensive gathering of circular fibers into large numbers of small narrow sheets.

Sulcus intermedius present, broad and shallow; sulcus angularis relatively deep, occurring just proximal to pyloric bend; tubular region of stomach extremely long and comprising nearly three-fourths total length of the stomach; pyloric bend considerably distant from cardiac junction, terminal third of stomach sharply recurved craniad and laterally toward

cardiac vestibule; terminal stomach tapering gradually from cardiac vestibule to sulcus angularis just proximal to bend and remaining narrow to pyloric sphincter, with musculature moderate and relatively uniform in depth throughout tubular portion. Pyloric sphincter thin, slightly more massive on greater than lesser curvature, directed into lumen of duodenum in both specimens observed; sphincter composed of circular layer and muscularis mucosae; pyloric mucosa lining sphincter deep; external constriction at sphincter slight; pyloric tube distal to bend approximately parallel to cardiac vestibule, hence direction of gastric orifices approximately equal with both directed anteriorly *in situ*.

Entire inner surface area of stomach covered with mucosal lining with pattern of rugal folds similar to that found in *Glossophaga;* submucosa scanty throughout, included within rugae and best developed within pyloric zone.

Musculature.—Both major muscular layers shallower throughout lesser curvature than elsewhere (excepting prominent thickening of wall at pyloric bend within lesser arc); muscularis externa extremely thin through cardiac vestibule along left wall, circular layer the deepest layer throughout; muscle wall moderate in depth through lesser curvature to pyloric bend, thickened slightly at bend to pyloric sphincter. External layers generally equal in depth throughout fundic caecum with circular layer thickened slightly at bases of rugae; wall of fundic caecum slightly thicker than that of lesser curvature. Longitudinal layer deeper relative to circular layer through more of stomach than in any other bat examined; fibers unusually oriented and prominently compartmentalized as discussed previously throughout fundic caecum, caecum appearing unusually elastic; muscularis externa of greater curvature lateral to fundic caecum relatively uniform in depth to pyloric sphincter, with no substantial thickening of either external layer in pyloric tube and no gathering of circular fibers into bundles in lateral two-thirds of tubular stomach. Muscularis mucosae thin, double layered, slightly deeper within rugae in comparison to stomach wall proper. Depth longitudinal layer 10 (cardiac vestibule) to 80, circular layer 25 (cardiac vestibule) to 150, muscularis mucosae 10 to 15.

Organization of gastric mucosa.—Orientation of mucosal folds similar to that of *Glossophaga* but longitudinal orientation better developed along ventral and dorsal walls of caecum; folds gathered longitudinally within most of tubular stomach and all of cardiac vestibule; folds more or less longitudinal throughout upper two-thirds of caecum, with pronounced zig-zag orientation and directed transversely into many short folds along posterior wall within lower third; dorsal surface of caecum dilated with radially arranged rugae similar to those in *Glossophaga*. Zones of gastric mucosa distributed in pattern similar to those of other frugivorous and necti-

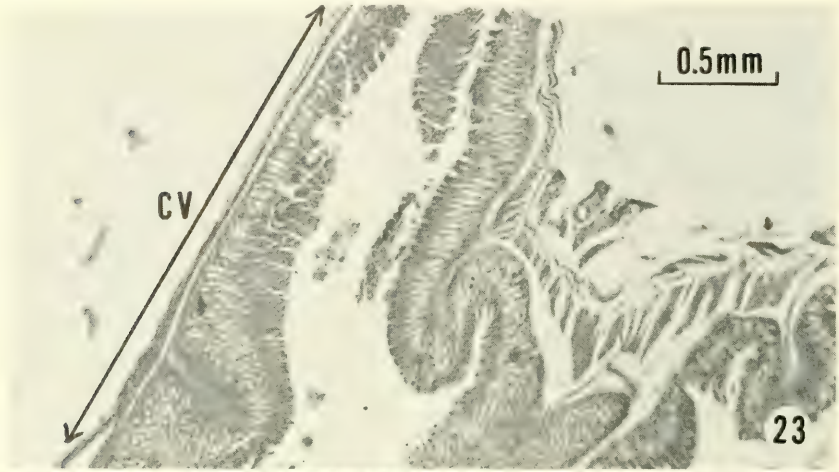
vorous phyllostomatids, but transitional zone relatively long and confined to narrow area proximal to pyloric bend on lesser curvature and more extensively distributed through pyloric bend on greater curvature; reduction in number of parietal cells abrupt within transition, but loss of zymogenic cells more gradual, occurring within proximal half; fundic zone more extensive on greater than lesser curvature with morphology of fundic glands highly variable from one region to another, and unusual in several structural features (refer to section on fundic mucosa); extensive variation in depth, mucosa slightly shallower within fundic caecum than remainder of zone; pyloric zone longer than in *Glossophaga,* occupying all of terminal segment of pyloric tube to rim of pyloric sphincter. Mucosa consistently deeper than that of *Glossophaga* relative to overall size of stomach; deepest within tubular portion of fundic mucosa and basal half of cardiac vestibule, decreasing only slightly in depth toward lateral extremities; mucosa shallowest within furrows between rugae (most apparent in caecum); mucosa along lesser curvature about same depth as that along greater curvature.

Cardiac glands.—Similar to those of *Glossophaga* in cellular structure and morphology of gastric pits; glands confined to narrower zone than in *Glossophaga,* tubules somewhat narrower, and lamina propria less abundant at bases of glands; junction with stratified squamous epithelium abrupt; glandular zone consistent in length throughout vestibule; depth approximately 90.

Fundus.—Fundic mucosa characterized by distinctive variability in surface epithelium and by extensive variability in numbers of various cellular components beneath surface epithelium from apex of fundic caecum to pyloric mucosa. Depth of fundic mucosa 220 to 370.

Zymogenic cells in marked abundance only within fundic caecum and proximal-most portion of tubular fundus (occupy up to basal 40%, gradually reduced in frequency laterally toward pylorus); parietal and mucous neck cells increase in abundance toward pylorus with parietal cells increasing mostly within middle portion of gland and mucous cells progressively increasing in abundance throughout entire length of gland; parietal cells nearly absent within apical arc of fundic caecum (only three or four cells persisting within central area of gland at extreme apex of fundic caecum), increasing tremendously from apex of caecum to termination within pylorus (heaviest concentration in mid-stomach and in upper midportion of tubule throughout most of fundic mucosa), progressively decreasing toward base of gland, occasionally scattered among basal chief cells within tubular fundus only.

Chief cells unusual in structure and arrangement; small and uniform in size; nuclei large, spherical, usually centrally located; cells more or less



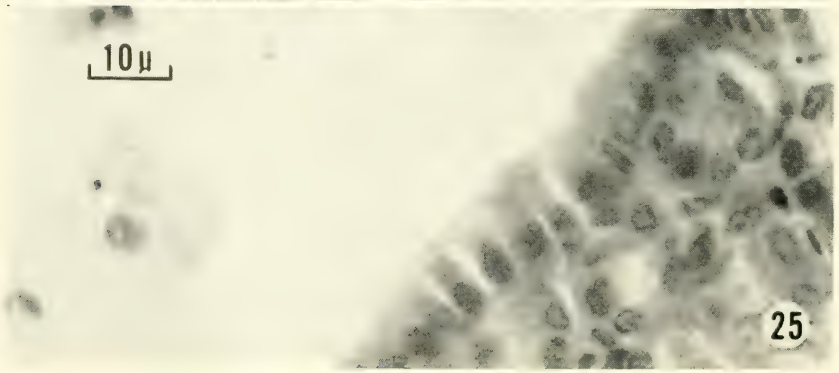


FIG. 23. Cardiac vestibule (CV) of *Carollia perspicillata.*
FIG. 24. Fundic caecum of *Carollia perspicillata.*
FIG. 25. Surface epithelium of the fundic mucosa in *Carollia perspicillata.*

columnar in shape, inner borders forming narrow but straight lumen (not observed in complexes of chief cells of other bats examined); basal portion of gland containing only slightly bulbular zymogenic cells.

Parietal cells exhibiting cline in size within gland, as well as cline in abundance within fundic zone; lower cells smallest, increasing in size to neck of gastric pit although never truly large relative to tubule breadth; parietal cells usually ovoid with large spherical to ovoid nuclei (nuclei generally decreasing in size toward lumenal surface).

Argentaffin cells observed infrequently among chief cells; triangular with clear cytoplasm excepting small amount of peripheral granulation at one corner of triangle.

Mucous neck cells substantially more abundant than chief cells in caecum, decreasing sharply in abundance toward pylorus (corresponding increase in parietal cells, coupled with progressive decrease in depth of gastric pits); cellular morphology of mucous neck cells located among parietal cells identical to that described for *Glossophaga*. Gastric pits extremely deep and broad within fundic caecum owing to unusually thickened surface epithelium and gastric pit cells; surface epithelium deep throughout stomach (Fig. 25), although especially so within caecum; pits 50-60% length of glands at apex, decreasing abruptly within middle portion of caecum, shallow (15-20% length of glands) through remainder of fundic mucosa and transitional area; pit cells large and cuboidal, increasing in size toward surface of mucosa, nuclei enormous and spherical. Surface epithelium composed of extremely elongate columnar cells in single layer with large, laterally compressed nuclei; surface cells decreasing in depth through tubular portion of fundus and becoming again thickened within pyloric mucosa. Lamina propria beneath glands typically scant; numerous smooth muscle fibers between glands within fundic caecum arising from muscularis mucosae, and distinctively more abundant than in other bats studied.

Pylo-fundic transition.—Narrow zone, although relatively broad among phyllostomatids studied; extensive on greater arc (parietal cells decrease gradually in number toward sphincter with occasional cells lingering through pyloric bend); parietal cells that persist in pylo-fundic region not confined to specific region within subepithelial portion although usually basal; loss of parietal cells more abrupt on lesser arc than greater curvature; chief cells disappear abruptly throughout lateral margin of fundic zone; gastric pits gradually increase in depth with changes in complements of cellular components; pyloric glands notably decrease in depth (in comparison to fundic mucosa) with reduced depth of terminal transitional mucosa reflecting this decrease; surface epithelium deepens abruptly at terminal margin of zone with no evidence of thickened epithelium within transition zone; complement of lamina propria as in fundic mucosa; depth 180 to 250.

Pyloric glands.—Distribution similar to that found in other frugivorous and nectivorous phyllostomatids although somewhat more extensive than in *Glossophaga;* occupying pyloric tube distal to bend; glands short, relatively straight and tubular, shallowest within inter-rugal furrows. Extensive differential gradient in cell morphology from base to surface of mucosa; basal cells small with large nuclei, essentially like those within glands of *Glossophaga* and upper cells progressively larger with slight decrease in nuclear size and nuclei occasionally compressed laterally. Lumen broad and increasing in breadth toward surface; surface epithelium unusually thick, comparable to that above fundic mucosa of caecum; unusually extensive layer of areolar connective tissue underlying pyloric glands, restricted to pyloric mucosa and with large number of interspersed mast cells and slight increase in interposed collagenous fibers compared to remaining mucosa (depth of connective tissue layer approximately 30). Depth of pyloric glands 130 to 200.

Glands of Brunner.—Extremely limited in distribution, occurring as single narrow clump on distal surface of pyloric sphincter, and with occasional scattered glands within mucosa along proximal surface of sphincter within pylorus but never within mucosa of stomach wall; glands extremely short and broad, highly convoluted; in highest concentration along lip of sphincter and decreasing gradually in depth to lateral junction of stomach and duodenum; cells large, pyramidal with small ovoid, peripheral nuclei; glands most limited in distribution of any bat examined.

Remarks.—The stomach of *Carollia perspicillata* somewhat resembles in general outline that of *Glossophaga soricina.* The extent of development of the fundic caecum is comparable to that of *Glossophaga,* although the caecum is less obviously distinguished from the remaining stomach by a sulcus. The distribution and orientation of mucosal folds is similar to that observed in *Glossophaga,* but there is somewhat more tendency toward longitudinal orientation within the dorsal and ventral surfaces of the fundic caecum. *Carollia* and *Glossophaga* also share the deep surface epithelium within the fundic caecum, and a marked variation in distribution of parietal cells within the fundic mucosa.

Carollia is unique in the patterns of distribution of zymogenic and parietal cells within the fundic stomach. Chief cells are commonest within the fundic caecum (often reduced in this area in other bats) and decrease progressively in number laterally, toward the terminal portion. Correspondingly, parietal cells are nearly absent in the fundic pouch, increasing in abundance to the termination of the pylo-fundic transition zone.

The tendency within the Phyllostomatidae toward elongation of the terminal stomach is marked in *C. perspicillata.* Recurvature of the relatively long terminal endpiece is so sharp that it curves back on itself. Speculations

regarding the possible functional significance of this recurvature follow in a later section.

Structural features at the aboral end of the stomach are strikingly like those of *Artibeus*. The pyloric valve is long and thin, directed into the duodenal lumen in both species. The glands of Brunner differ slightly histologically but in both species are confined to small masses at the distal surface of the pyloric sphincter with few within the submucosa of the duodenal wall.

Subfamily Sturnirinae

Sturnira lilium (E. Geoffroy-St. Hilaire, 1810)

Specimens examined (3).—Three specimens of *Sturnira lilium parvidens* from Nicaragua (KU 106086, 106102, 106104).

Overall dimensions.—Greatest length 9.0-10.2; greatest breadth 6.0-6.3; gastroesophageal junction to pyloric valve 4.7-4.9; gastroesophageal junction to apex of fundic caecum 4.8; breadth of pylorus at sphincter 1.2-1.3.

General morphology.—Small, slight curvature along back (dorsal) surface, hence concave dorsally; fundic caecum saccular; cardiac vestibule long and tapering; elongate, narrow pylorus recurved craniad; mucosal folds gathered in unusual direction. Gastroesophageal junction markedly superior to pyloric sphincter and junction with cardiac mucosa abrupt; no evidence of anatomical cardiac sphincter; cardiac vestibule (Fig. 26) extremely long, thin walled, expanding gradually from gastroesophageal junction to terminus in lesser curvature, oriented in S-configuration with cardiac orifice directed antero-laterad approximately as pyloric orifice; wall of cardiac vestibule more extensive along surface toward pylorus than that adjacent to upper caecum. Fundic caecum extremely saccular and thin walled; expanded on both upper and lower surfaces into spacious chamber with rounded apex; dorsal surface expanded; fold of stomach wall along rear (dorsal) surface that distinguishes cardiac vestibule and caecum. Incisura cardiaca deep and narrow; occurring as distinctive depression only within posterior half of stomach with slight thickening of circular muscle layer at base of incisura, and with orientation of circular muscle fibers separated into sheets by septa; prominence of incisura attributable to notable anterior dilation of fundic caecum. Tubular stomach distal to fundic caecum exceptionally long and narrow; terminal half of tubular region at 90-degree angle to remaining stomach and distal-most half with pyloric sphincter recurved craniad; pyloric bend gradual; tapering gradually to pyloric bend then relatively uniform in breadth to pyloric sphincter. Musculature of pyloric sphincter poorly developed throughout, least well represented on lesser curvature (reduced to simple "ridge" of circular muscle in most places and occasionally totally absent in portions of its circumference); circular muscle and muscularis mucosae contributing to sphincter but

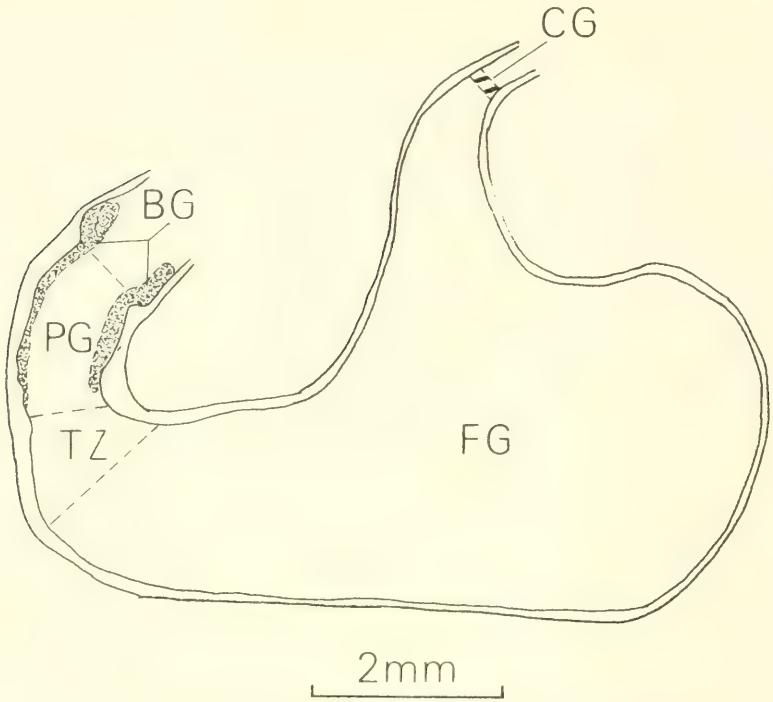


FIG. 26. Mid-longitudinal representation of the stomach of *Sturnira lilium*. For explanation of symbols, see Figure 3.

overlying mucosa deep along muscular ridge, hence total sphincter mass extensive; external constriction at sphincter slight; sulcus intermedius present at pyloric bend not prominent. Lamina propria extremely rare everywhere within stomach wall (except beneath muscularis mucosae within pyloric mucosa), prominent within rugae (greatest within terminal portion of pyloric tube); rugal folds and gastric mucosa well developed throughout, no apparent secondary reduction of either; mucosa especially deep within cardiac vestibule.

Musculature.—Longitudinal and circular layers thin throughout fundic caecum and cardiac vestibule, with local thickening of circular layer at bases of rugae; gathering of circular fibers into bundles pronounced only within lower wall of caecum and occurring to a lesser degree within midregion of greater curvature. Circular layer always thicker than longitudinal layer, with regions of thickened circular muscle confined to tubular stomach (originating on lesser curvature at base of cardiac vestibule, then increasing gradually in depth to maximum at pyloric bend, then decreasing slightly again to second thickening at pyloric sphincter); essentially identical pattern as above within greater curvature, although musculature consistently thicker

than in lesser curvature in corresponding areas. Longitudinal layer a thin sheet throughout stomach, including pyloric tube, not contributing to sphincter. Muscularis mucosae a thin double layer throughout with little submucosa beneath and most prominent in pyloric area. Ganglia of Auerbach's plexus abundant only within pyloric tube and greatest within greater curvature. Depth longitudinal layer 15 to 20, circular layer 20 to 150, muscularis mucosae less than 10.

Organization of gastric mucosa.—Mucosa gathered uniformly into longitudinal, parallel folds throughout tubular portion of stomach and cardiac vestibule, with slight interdigitation of basal-most rugae in vestibule; mucosa of fundic caecum arranged in interdigitating network of deep rugal folds with net direction of orientation more or less longitudinal (apex of fundic caecum toward pyloric tube), but some secondary transverse orientation apparent; interdigitation of folds confined to saccular fundus proper, fundic mucosa of mid-stomach gathered longitudinally with little or no gathering into short discontinuous folds along arc of greater curvature; remaining mucosa consistently gathered on long, continuous ridges traversing greater part of length of stomach.

Fundic mucosa uniformly shallow on apexes of rugae within fundic caecum and mid-stomach, no local reduction within apex of caecum and notably deepest throughout cardiac vestibule where glands are consistently longest and narrowest; pyloric glands notably shallower than fundic or cardiac mucosa, although mucosal membrane of pyloric tube exceptionally thick owing to underlying layer of glands of Brunner; both fundic and pyloric mucosa thicker on lesser curvature than greater.

Four glandular types recognized within mucosal membrane including glands of Brunner (submucosal in duodenum) beneath certain portions; cardiac glands confined within typically narrow belt at gastroesophageal junction, zone equal in length throughout; fundic mucosa occupying all of cardiac vestibule and saccular fundus, and mid-stomach up to depletion of chief cells proximal to pyloric bend; transitional area narrow and unequally distributed on lower surfaces, confined to narrow region within pyloric bend; pyloric mucosa occupying entire surfaces of short pyloric tube distal to pyloric bend and extending slightly beyond pyloric sphincter into duodenum; glands of Brunner present in typical distribution at superior end of duodenum but also occurring within gastric mucosa beneath entire pyloric gland complement and most of pylo-fundic transition area, gradually decreasing in abundance from gastroesophageal junction through pylorus to termination within pyloric bend; no intergraduation of basal Brunner's glands with zymogenic cells of fundus, hence junction abrupt.

Cardiac glands.—Short, thin and tubular within narrow zone at gastroesophageal junction; junction with stratified squamous epithelium abrupt;

glands narrow and composed of single cell type; glands two to three times breadth of adjacent fundic glands; mucous cells extremely large (twice size of surface epithelial cells of remaining stomach); cells pyramidal with small, ovoid nuclei within lower half of cell (not juxtaposition to basal membrane), cells increasing in size from base to surface; mucous border deep; lumen extremely broad and expanded at base along with gland; transitional zone to fundic mucosa absent; glands distinctive in morphology, easily distinguished from remainder of gastric mucosa; depth 60, breadth of zone 30.

Fundus.—Glands extend throughout all of saccular and tubular stomach up to pyloric bend; glands uniform in basic morphological pattern, but varying slightly in depth and breadth in cardiac vestibule in comparison to remainder of fundic stomach. Glands generally short and broad with extremely shallow gastric pits; chief cells extensively distributed within gland, succeeded by thin but distinctive zone of primarily mucous neck cells superior to chief cell complex, with parietal cells confined mostly to upper half and most prominent immediately beneath gastric pits; no distinctive reductions in depth of mucosa anywhere within mucosa including fundic caecum; mucosa of cardiac vestibule considerably deeper than remainder of fundus, owing to substantial increase in relative numbers of parietal cells, and also gastric pits somewhat lengthened. Depth of fundic mucosa 120 to 170 within tubular stomach and fundic caecum and up to 220 in cardiac vestibule.

Basal zymogenic cells extensive in numbers within glands and generally throughout fundic region, may occupy up to 60% length of gland (normally basal 40-50%); zymogenic cells large, polyhedral, irregular in size, little apparent size gradient within gland; nuclei small and ovoid to spherical, peripheral although not necessarily juxtaposed to basal membrane; large and extensive chief cells result in notable basal expansion of fundic glands, chief cell complex most conspicuous element within glands. Cells strictly definable as argentaffin cells not observed but presumed present.

Mucous neck cells particularly abundant within medial 20% of gland, large and with small peripheral, spherical nuclei; clear, relatively extensive cytoplasm; upper mucous neck cells among parietal cells smaller with larger nuclei and wedged between adjacent parietal cells.

Parietal cells long, narrow, ovoid and with oval nuclei; nuclei vary considerably in size and often displaced peripherally; size gradient within cell distribution present but not pronounced; cells confined mostly to upper half of gland and increase progressively in frequency to maximum directly beneath gastric pits; parietal cells occurring infrequently among zymogenic cells; relatively uniform in numbers throughout fundic mucosa although somewhat more abundant within cardiac vestibule than remainder of area.

Gastric pits shallow, although somewhat variable in depth, usually occupying upper 10-15% total length of gland; cells small with large consistently spherical nuclei throughout pit (no lateral compression); lumen narrow; surface epithelium shallow and cells small with spherical nuclei, mucous border not deep.

Pylo-fundic transition zone.—Narrow zone at pyloric bend, more extensive on greater than lesser curvature; unusual in having glandular portion in form of cellular elements identical to glands of Brunner; transitional glands generally intermediate in height between fundic and total pyloric mucosa (inclusive of basal cells of Brunner's glands); depletion of zymogenic cells abrupt at beginning of zone, with parietal cells persisting throughout as small remnants confined to area above basal mucous elements and decreasing in number gradually toward pyloric sphincter; parietal cells not observed among basal mucoid cells (presumed glands of Brunner) with no region of gastric mucosa existing in which parietal cells extend to base; gastric pits increase gradually in depth with progressive loss of parietal cells; surface epithelium identical to that of pyloric area, shallow, with small cells having small and spherical nuclei; depth 180 to 200.

Pyloric glands.—True pyloric mucosa restricted to short pyloric tube distal to pyloric bend; glands stunted owing to layer of underlying glands of Brunner; narrowly expanded into bulb at base, sharply increasing in breadth from midregion to surface epithelium, resulting in funnel-shaped appearance; depth variable, generally increasing gradually from origin within pyloric bend to termination at pyloric sphincter; composed of single cell type; cells small and with extremely large spherical nuclei which decrease slightly in size to surface epithelium and never are laterally flattened; cells narrow and elongate with extensive mucous border; lumen broad, increasing gradually toward surface; thin layers of connective tissue and smooth muscle fibers derived from muscularis mucosae separating pyloric glands from underlying glands of Brunner; surface epithelium relatively thick when compared to that of adjacent transitional glands; lamina propria thin layer beneath pyloric glands; basal glands of Brunner discussed in following section; pyloric glands do not penetrate into lumen of duodenum; depth 100 to 240 (not including basal glands of Brunner).

Glands of Brunner.—Moderate in abundance within duodenum, occupying proximal 1.5 mm and occurring in single mass continuous with complement in stomach; heaviest concentration at sphincter; tubules decreasing progressively in length toward termination in duodenum; submucosal within duodenum.

Glands occupy basal position within mucosal membrane of pyloric and, to lesser extent, pylo-fundic transition area (Figs. 26, 27); both mucosal and submucosal within pylorus (beneath muscularis mucosae), although

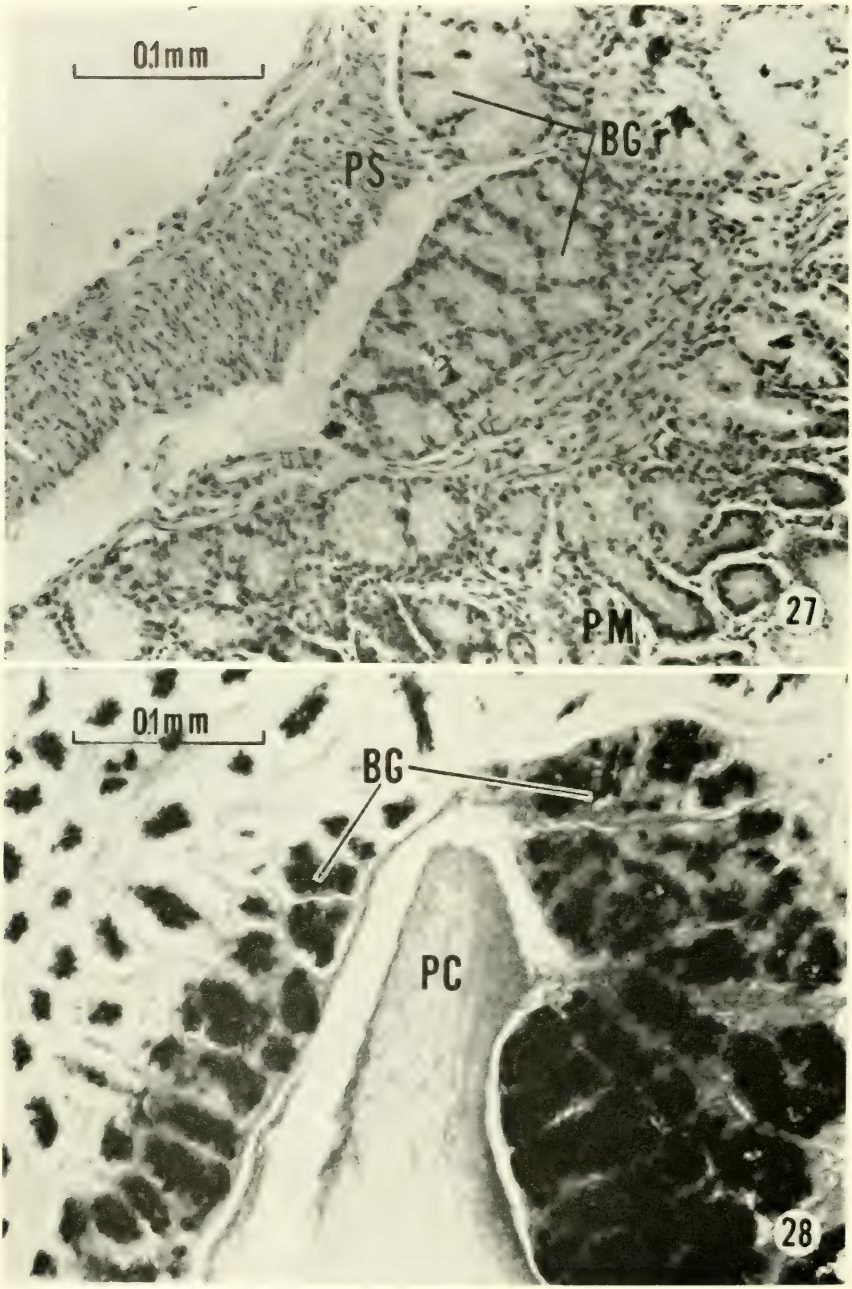


FIG. 27. Glands of Brunner (**BG**) within the pyloric mucosa (**PM**) of *Sturnira lilium;* the pyloric sphincter (**PS**) also is seen.

FIG. 28. Glands of Brunner (**BG**) within the pylorus of *Sturnira lilium* showing reaction to PAS; the pyloric constriction (**PC**) marks the limit of the pyloric stomach (left of constriction).

usually observed superior to muscularis mucosae (Fig. 28); increase progressively in depth from origin at pyloric bend to distribution within duodenum.

Morphology of glands identical throughout (Fig. 27); tubules highly convoluted, branching into two or three units and consistently large throughout entire distribution; tubules open lumenally by way of pores between adjacent pyloric glands or crypts of Lieberkühn depending upon location within gastrointestinal tract; tubules never an anatomical subunit of any other glandular type; cellular morphology of Brunner's glands consistent throughout distribution; cells large, pyramidal, with light granulation; nuclei extremely small, juxtaposed to basement membrane, moderately to heavily compressed laterally; glands large in comparison to most other bats examined and with expansive lumen; muscularis mucosae and lamina propria comparatively well developed beneath pyloric complement of Brunner's glands.

Remarks.—*Sturnira* demonstrates the most pronounced invasion of the glands of Brunner into the pyloric stomach of any bat examined. Although this condition is not restricted to this species, it is most obvious and best developed here. It is interesting to note that in addition to having large numbers of Brunner's glands beneath the entire distribution of pyloric mucosa, the pyloric sphincter is distinctively reduced, and indeed virtually absent in portions of the gastroduodenal junction. This condition suggests that the invasion orally of Brunner's glands may be partially a developmental by-product, in the absence of a prominent barrier conceivably produced by a muscular pyloric sphincter. Although *Molossus*, with its prominent pyloric sphincter, also apparently has Brunner's glands beneath the pyloric mucosa, the condition is qualitatively and quantitatively much less distinctive than in *Sturnira*. Investigations of gastrointestinal development in bats should prove useful in determining any relationship between the size of the pyloric sphincter and the extent of Brunner's glands. To my knowledge, the studies herein reported include the first mention of a distinctive complement of the glands of Brunner in the stomach of a placental mammal.

The musculature of the stomach wall of *Sturnira* is similar to that observed in other non-carnivorous phyllostomatids—thin and with the circular layer arranged locally into bundles enclosed by thin, tissue-like septa.

Subfamily Stenoderminae

Artibeus lituratus (Olfers, 1818)

Specimens examined (3).—One specimen from Chiapas (uncatalogued) and two from Nicaragua of *Artibeus lituratus palmarum* (KU 106221, 106236).

Overall dimensions.—Greatest length 11.6-13.5; greatest breadth 8.0-8.7;

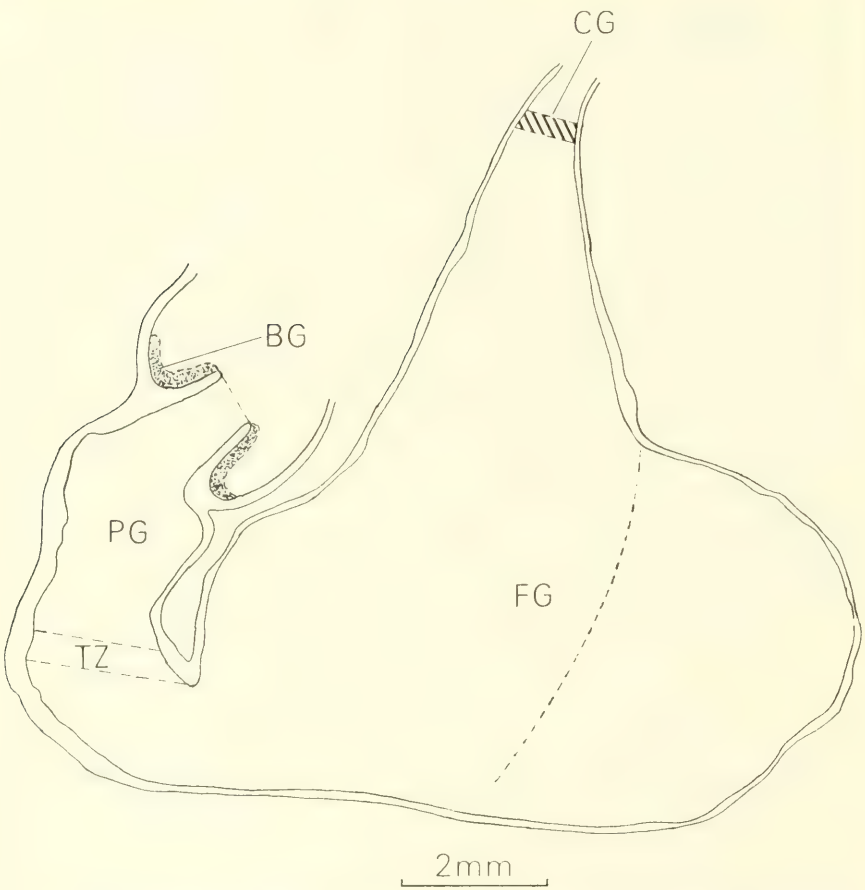


FIG. 29. Mid-longitudinal representation of the stomach of *Artibeus lituratus*. For explanation of symbols, see Figure 3.

greatest breadth of fundic caecum 5.5-6.0; gastroesophageal junction to pyloric valve 6.0-6.1; gastroesophageal junction to apex of fundic caecum 8.4-9.1; breadth of pylorus at sphincter 1.6-1.7.

General morphology.—Similar in many gross morphological features to stomach of *Sturnira lilium*, although considerably larger and extremely saccular, with unusually large fundic caecum and long, broad cardiac vestibule; dorsal surface concave and with marked dorsolateral curvature of entire stomach.

Pyloric tube relatively long and narrow (Fig. 29), recurved sharply anteriorly distal to pyloric bend; musculature thick; pronounced sulcus intermedius in central portion of tube; marked external pyloric constriction at sphincter; nearly entire internal surface of terminal endpiece lined with

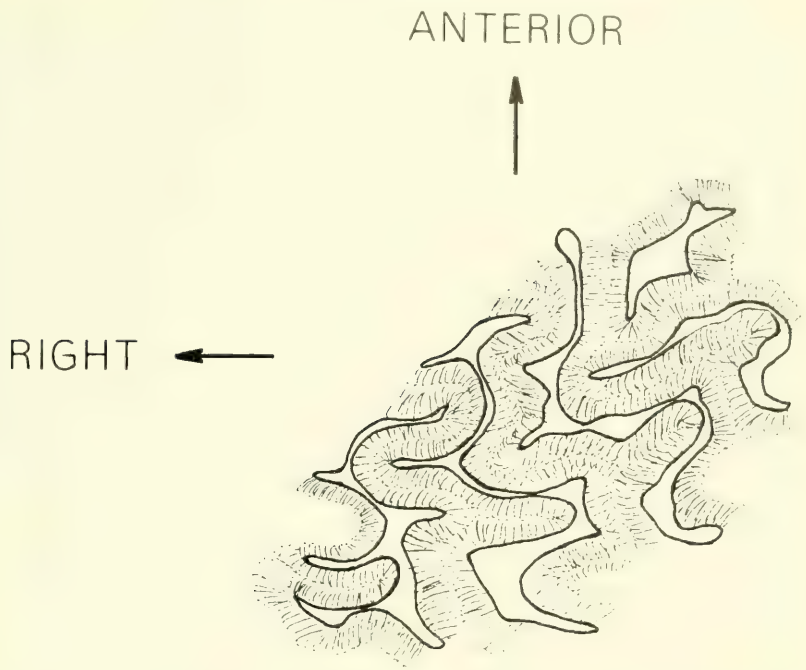


FIG. 30. Diagram showing anastomosing rugal folds with extensive interdigitation of ridges in the fundic stomach of *Artibeus lituratus*. Note the anterior-posterior, rather than longitudinal (left to right) direction of the folds.

pyloric-type mucosa; rugae (Fig. 30) and inclusive muscularis mucosae and lamina propria unusually well developed along greater arc of pyloric tube beneath pyloric glands, underlying submucosa unusually well developed in pylorus; phyloric sphincter (Fig. 31) of circular muscle and muscularis mucosae with slight contribution of longitudinal muscle layer at extreme base of sphincter, gastric mucosa well developed on musculature of valve, sphincter muscle broad at duodenal lumen in preserved specimens, sphincter muscle broad at origin on stomach and tapering to narrow endpiece medially, sphincter symmetrical; sphincter funnel-shaped rather than disc-shaped and must produce effective seal upon contraction of circular muscle if functional; pyloric orifice displaced considerably inferior (4-5 mm) to cardiac orifice with both directed in nearly same direction.

Incisura cardiaca present but poorly developed. Cardiac vestibule (Fig. 32) massively developed in all directions into distinct chamber (externally) originating at narrow gastroesophageal junction and increasing gradually in breadth to lower terminus within lesser curvature; vestibule in one specimen with slight S-configuration, anteriormost region reflected laterally and parallel to pyloric tube (probably result of slight "tilt" of stomach *in situ*).

vestibule expanded frontally yielding greater external as well as internal distinction to region than in *Sturnira;* cardiac orifice substantially superior to pyloric orifice.

Vestibule emptying into greatly dilated saccular fundus divisible into two general areas, 1) central portion between pyloric bend and fundic caecum and 2) extensively dilated fundic pouch; fundic caecum extremely large, more rounded on dorsal surface (*in situ*) than in *Sturnira;* tapering laterally to narrow apex, distinguished from remaining fundus by fold in stomach wall on dorsal surface as in *Sturnira;* gastric mucosa not decreasing in depth within caecum, thin walled.

Lamina propria somewhat more abundant than in most other bats examined but non-muscular submucosa generally thin throughout (with exception of pyloric tube, and within and at base of rugae in fundic caecum, where loose connective tissue often dense and moderately abundant). Stomach clearly adapted for acceptance of, and perhaps storage of, large amounts of food.

Musculature.—Muscle layers of fundic caecum and fundus of mid-stomach irregular in depth and morphology as in *Sturnira;* stomach wall extremely thin throughout most of fundic stomach and cardiac ampulla (except for circular layer at origin of rugal folds where internal muscle layer notably thickened and grouped into large bundles surrounded by thin septa of connective tissue); musculature especially thin in cardiac vestibule; circular muscle also thickened at base of rugae, single large blood vessel observed within lamina propria at base of, and ascending into, each rugal fold with system best developed in fundus, to lesser degree in pyloric tube.

Longitudinal muscle layer uniformly thin throughout most of stomach, slightly thickened in pyloric tube in comparison to remaining stomach.

Circular muscle greatly thickened thoughout greater curvature of pyloric tube, decreasing gradually in depth through pyloric bend; circular muscle of lesser wall of pylorus thickened locally proximal to pyloric sphincter, thin throughout remainder of pylorus; lamina propria above circular layer relatively thick within greater arc of pylorus.

Muscularis mucosae forming generally thin sheet beneath gastric mucosa but thicker beneath gastric mucosa and within rugal folds of pyloric tube. Musculature of gastroesophageal junction thin, lacking local thickening except for definite bundling of circular layer; no conclusive evidence suggesting presence of active cardiac sphincter, although local segregation of circular muscle fibers reveals presence of questionable morphologic specialization. Depth longitudinal layer 20 to 30, circular layer 20 in fundic caecum to 185 in pyloric tube, muscularis mucosae 10.

Organization of gastric mucosa.—Mucosa arranged throughout fundic stomach into large, complex, interdigitating networks of folds (more com-

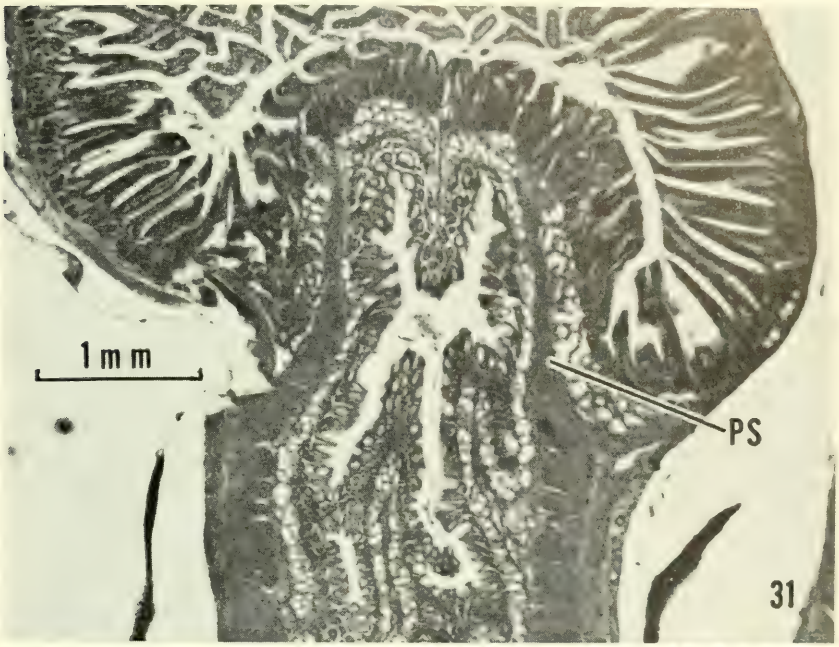


FIG. 31. Pyloric sphincter (**PS**) of *Artibeus lituratus*.

FIG. 32. Cardiac vestibule of *Artibeus lituratus* showing fold in body wall (**FO**), duodenum (**DUO**), and cardiac vestibule (**CV**). Anterior is to the left in this photograph.

plex than in *Sturnira*) with more or less regular pattern as illustrated in Figures 30, 32; general direction of orientation antero-posterior, angled such that folds progress antero-posteriorly, but directed upward and to the right; interdigitation more pronounced in fundic caecum than remainder of fundus; folds in pyloric tube irregular in shape, clearly directed more longitudinally than those of fundus and not interdigitating. Mucosal folds generally extremely well developed without local reductions anywhere in fundus, although slightly shallower pyloric glands on musculature of pyloric sphincter than elsewhere; mucosa unusually uniform in depth throughout fundus, including furrows between folds, less uniform in pyloric tube owing to thickening on sides of rugae and reduction in depth within furrows between adjacent folds.

All glandular types present, although pylo-fundic transitional glands reduced to remnant; cardiac glands occupying narrow belt at gastroesophageal junction; fundic glands occupying all of remaining surface area except pyloric tube; fundic glands long and narrow, exhibiting notable specialization in distribution of cellular types; pylo-fundic transition zone extremely narrow, basal zymogenic cells of fundus extending to pyloric bend; pyloric glands extensive, unusual in appearing to consist of two cellular types, forming mass of enlarged pyloric sphincter.

Cardiac glands.—Narrow zone inferior to gastroesophageal junction; similar to pyloric glands in basic morphology, but only single cell type present; cardiac glands longer and broader than adjacent fundic glands, broadly expanded basally, cells long and narrow in single dense layer; nuclei spherical with marked size gradient of decrease from lower to upper part of glands; luminal mucous border extensive (over twice breadth of nucleus); broad foveolae plus extensive mucous border yielding relatively broad glands; junction with fundic mucosa abrupt; transitional element absent as zymogenic cells present within glands adjacent to lower cardiac elements; junction with esophageal epithelium equally abrupt; lamina propria beneath glands thin; depth 210 to 280.

Fundus.—Distribution of glands similar to that of *Sturnira;* mucosa deep and of rather uniform depth throughout stomach; extends from posterior limit of cardiac zone through cardiac vestibule and fundic caecum laterally to pyloric bend; arrangement of mucosal folds complex; glands long and extremely narrow, tightly compact, little or no apparent convolution, expanded at upper and lower ends but narrowing in midregion. Depth of fundic mucosa 160 to 180.

Zymogenic cells small, pyramidal with small, spherical nuclei (usually in outer periphery of cell but occasionally displaced medially); cells relatively limited in distribution within basal 15-20% of gland, never in complete

absence of parietal cells; uniform in distribution within all glands containing parietal cells. Argentaffin cells not observed but assumed present.

Parietal cells remarkably abundant, occurring throughout virtually entire length of gland to just beneath surface epithelium, most heavily concentrated in medial 60% where abundance virtually excludes mucous neck cells; cells unique among bats examined in being abundant among chief cells at base of glands (although less abundant than in medial portion) and somewhat less common immediately beneath gastric pits; cells generally large, circular, uppermost cells often four times breadth of those at base, occasionally as broad as gland itself; nuclei also large, usually ovoid, most often peripheral with nuclei of basal-most cells extremely large and ovoid.

Mucous neck cells extremely small and sparsely distributed among parietal cells; less frequent than parietal cells in medial half of gland where usually located along inner surface of tubule; nuclei spherical and smaller than those of parietal cells.

Gastric pits extremely short and thick-walled, up to 15% length of gland but usually less; cells lining pits large, densely packed, with large nuclei and lumen narrow; surface epithelium extremely thick, represented by dense clumps of epithelial cells with large, club-shaped nuclei.

Pylo-fundic transition zone.—Region so narrow as to appear nearly absent; replacement of parietal cells by mucous neck cells abrupt in pyloric bend; zymogenic cells present in base of glands in proximity of pyloric mucosa, although reduced in abundance; gastric pits abruptly deepened at terminal border of transition zone; depth about 170.

Pyloric glands.—Extensive and well-developed area occupying most of tubular stomach distal to pyloric bend and terminating aborally at apex of lip of pyloric sphincter; differing distinctively in morphology and dimensions from remaining gastric mucosa including cardiac glands; pyloric glands consisting of two apparent cellular types; approximately lower third occupied by small light-colored cells with small round nuclei and slight cytoplasmic granulation; lower portion of gland bulbular; cells of upper two-thirds larger and more ovoid, mucous border twice as broad as in lower cells; basal cells clearly unique within mucosa and notably similar to cells of Brunner's glands; pyloric glands long and broad, nearly twice as broad as cardiac glands; surface epithelium thicker than that of fundus, nuclei laterally flattened, mucous border extensive. Lamina propria unusually well developed along with submucosal elements in general, especially in rugae; muscularis mucosae thick in rugae as well as stomach wall proper; loose submucosa relatively abundant beneath muscularis mucosae, typically infrequent above; extensive deposits of adipose tissue occurring in submucosa of pyloric tube (beneath muscularis mucosae) and to lesser extent in fundic stomach; connective tissue immediately beneath pyloric gland

tensive than in fundus. Glands more irregular in depth than those of fundic glands and reduced in depth within furrows between rugae and along surface of pyloric sphincter. Depth of pyloric mucosa 140 to 185.

Glands of Brunner.—Restricted to immediate vicinity of pyloric sphincter and fewest in number of any bat examined (excepting *Carollia*); occurring in narrow belt along distal surface of sphincter but not extending beyond lip of sphincter; large (more than twice breadth of pyloric gland), compound tubular, not highly convoluted; cells long and narrow with diffuse granulation, more like mucous cells of gastric mucosa than in other bats examined; nuclei small, spherical, basal, never laterally compressed; lumen large, as broad as single gastric gland, empties between crypts of Lieberkühn; glands unique in morphology among bats examined.

Remarks.—The stomach of *Artibeus lituratus* clearly is adapted to accept large quantities of food material and may well serve to retard, secondarily, its transport through the digestive system. Extensive development of the cardiac vestibule and fundic caecum can only suggest modifications to assimilate a bulky diet, probably normally fruit of trees and shrubs (Goodwin and Greenhall, 1961). Thin musculature of the entire non-pyloric stomach would allow for expansion, and thus for consumption of large quantities of food.

Several specializations occur that probably are related to retarding gastric flow through the stomach, a phenomenon not uncommon among mammals that feed primarily on herbaceous material. The orientation of mucosal folds (Fig. 30), for example, would provide a mechanism for directing some food material laterad into the unusually spacious fundic caecum, upon contraction of the stomach wall, with the thickened circular muscle bands within the bases of the rugal folds providing the necessary contraction. Unusually extensive development of the pyloric sphincter and tube may be modifications providing an effective closing mechanism against large quantities of food, although the importance of an anatomical pyloric sphincter in this regard may be in question in mammals (Selkurt, 1966). The pyloric tube is extremely narrow in relation to total stomach size and probably offers resistance to an escaping bolus.

The fundic mucosa exhibits reduction in numbers of zymogenic cells within individual glands, although presence of these cells is uniform throughout the entire region. Inasmuch as chief cells are the suspected site of secretion of pepsin, it is not surprising that they are less abundant in this primarily fruit-eating bat than in most other species studied. However, the unusual abundance of HCl-producing parietal cells is not clear. In addition to its function of providing the proper pH for activity of gastric proteases, hydrocloric acid also functions in prevention of bacterial growth and stimulation of secretion of secretin and pancreozymin in the duodenum, as well

as enzymes by the pancreas (Glass, 1968). Perhaps the extensive parietal cell complement in *Artibeus* can be linked to one or more of these secondary functions. No other species of bat examined exhibited such extensive numbers of parietal cells and, for the present, this feature must be considered unique in *Artibeus*.

Although unique with respect to certain features, the stomach of *Artibeus* is similar to that of other phyllostomatids in gross morphology. *Artibeus* resembles phyllostomatids generally in possession of a saccular, asymmetrically formed, muscular, and recurved pylorus, and thin musculature throughout a well-developed globular fundic caecum.

Although distinctive, the stomach of *Artibeus lituratus* is clearly similar topographically to that of *Sturnira lilium*. Similarities include the broad, elongate, slightly S-shaped cardiac vestibule, well-developed saccular fundic caecum, short and sharply recurved terminal endpiece, and (internally) the interdigitating, diagonally-oriented mucosal folds. Differences include a broad pylo-fundic transition zone and predominance of chief cells in the fundic mucosa in *Sturnira*, in contrast to an extremely narrow transitional element and persistence of parietal cells as the most conspicuous cell type of the fundic mucosa of *Artibeus*.

It is of some interest to note that Grassé (1955), in a classification of stomachs of bats into 1) megachiropteran, 2) microchiropteran and 3) *Desmodus*-type, included as primary features of the megachiropteran ("regimé frugivore") type a conical cardiac region (cardiac vestibule of Grassé), an extensive pyloric tube, and a spacious fundic caecum. Additionally, Grassé included an illustration (after E. Pernkopf) of the stomach of *Pteropus vampyrus*, an Old World frugivorous megachiropteran, that bears a resemblance to that of *Sturnira* and *Artibeus* in the features discussed above. Also, Grassé (1955) stated that the genus *Nyctimene*, a group of fig-eating megachiropterans of the subfamily Nyctimeninae, is exceptional among members of the suborder in possessing a simple globular microchiropteran-like stomach; Koopman (1967) and Walker (1968) noted that *Nyctimene* may include insects in the diet.

Examination of more species and numbers of individuals of each kind will be required before generalizations regarding coevolution of gastric structure and food habits are truly conclusive. Further study may shed light on the possibility of parallel evolution in gastric morphology in the Megachiroptera and Microchiroptera, as suggested above.

Subfamily Desmodontinae

Desmodus rotundus (E. Geoffroy-St. Hilaire, 1810)

Specimens examined (3).—Three specimens from Nicaragua of *Desmodus rotundus murinus* (KU 106260, 106262-63).

Overall dimensions.—Greatest length 75.0-86.0; greatest breadth 21.0-31.0;

gastroesophageal junction to pyloric sphincter 1.9-2.1; gastroesophageal junction to apex of fundic caecum 72.5-83.0; breadth of pylorus at sphincter 2.3-2.5.

General morphology.—Stomach modified into narrow, elongate caecum of relatively uniform breadth originating at gastroesophageal junction, with diverticulation of gastrointestinal tract into stomach and duodenum (Fig. 33); caecal pouch initially directed laterally (to the left), bending sharply caudad approximately 3 mm lateral to esophageal junction, continuing aborally to approximately midway along length, then recurving sharply craniad, and recurving again posteriorly just proximal to apex (Fig. 34); stomach uniformly narrow throughout most of length, dilated slightly near apex and slightly constricted within terminal 15 mm. Cardiac vestibule absent, squamous epithelium terminating symmetrically and abruptly at lesser curvature; aboral end of esophagus slightly expanded at junction; no evidence of anatomical cardiac sphincter; muscularis externa and muscularis mucosae of esophagus unmodified in dimensions or structure at junction with lesser curvature.

Pylo-duodenal junction and pyloric sphincter in close proximity and located at right angle to gastroesophageal junction; pylorus occupying region between pyloric sphincter and beginning of tubular fundic caecum (inclusive of mucous glands at gastroesophageal junction); valves of pyloric sphincter short and extremely thin, expanded slightly at apex, sphincter portion of muscularis externa composed only of circular muscle layer; remaining muscularis externa well developed (both layers); circular layer extremely complex and somewhat variable in depth; tunica propria extensively developed throughout stomach as dense layer between muscularis mucosae and circular layer (heavy complements between loosely organized bundles of circular fibers, elastic fibers rare among collagenous fibers); stomach most heavily vascularized among species examined with extensive numbers of arterioles and venules within areolar connective tissue.

Gastric mucosa unusual in that most glands reduced to simple alveolus or tubuloacinar type (Rouk, 1968); cellular complements reduced in number as compared to other bats examined.

Musculature.—Wall relatively uniform in depth throughout caecum but slightly reduced in depth along lesser curvature in vicinity of gastroesophageal junction. Longitudinal layer moderate in depth throughout gastric pouch and narrowest within dilated portion and at apex, occasionally observed broken into tightly packed clumps of fibers and sometimes appearing as two layers. Circular layer always deeper than longitudinal layer at given point; fibers of circular layer organized throughout stomach (excepting incisura cardiaca) into normally large, loosely arranged, transversely-oriented bundles (Fig. 35) surrounded on upper surface and sides

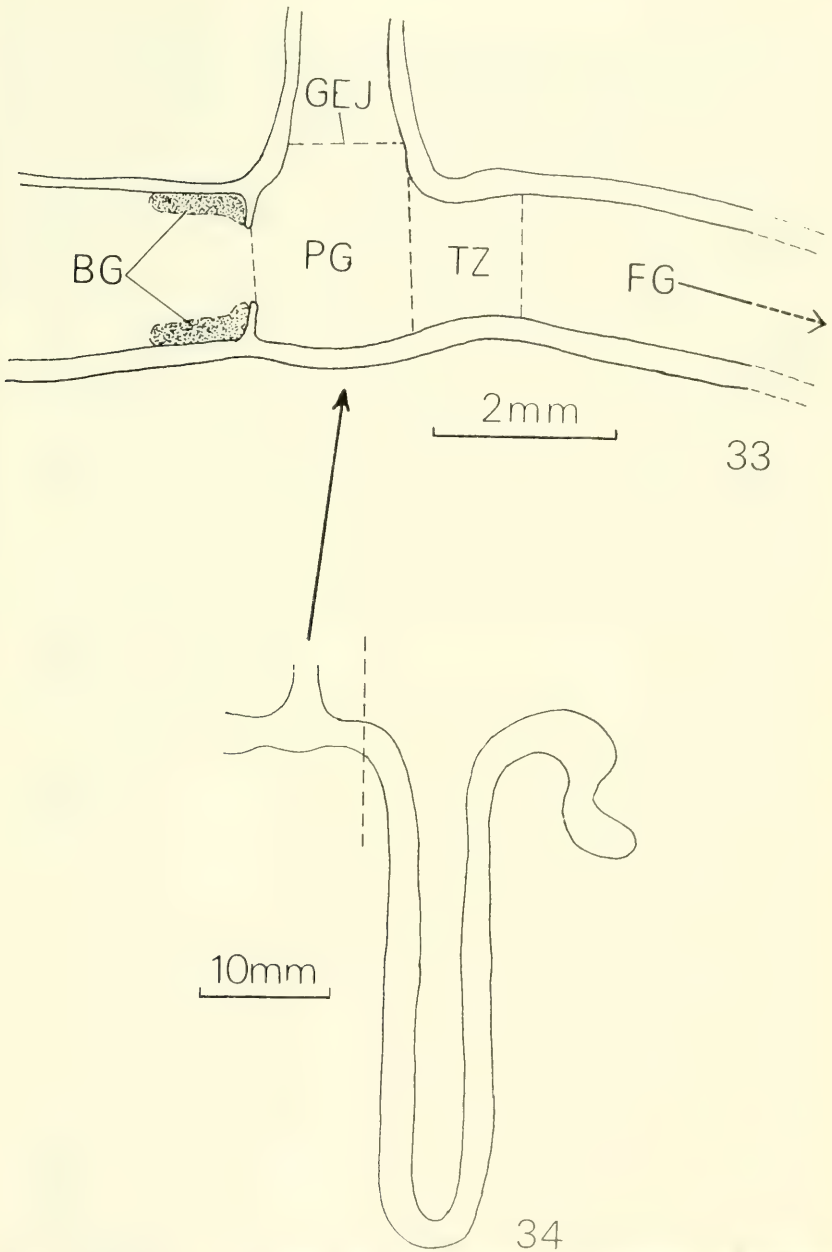


FIG. 33. Diagram of the cardiac and pyloric junctions of the stomach of *Desmodus rotundus*. Dotted lines indicate the continuation of the fundic caecum; it was not possible to include it to scale in this figure; **GEJ**, gastroesophageal junction. For explanation of other symbols, see Figure 3.

FIG. 34. Semidiagrammatic representation of the stomach of *Desmodus rotundus*. Note the local dilation of the caecum near the apex.

by extensive amounts of connective tissue; circular muscle bundles slightly variable in depth, no bundling at incisura cardiaca and gastroesophageal junction. Muscularis mucosae in extremely thin sheets and no deeper within rugae than stomach wall proper. Lamina propria mucosae extensive superior to circular layer. Depth longitudinal layer 15 to 30, circular layer 30 to 100 (usually 60 to 75), muscularis mucosae less than 10.

Organization of gastric mucosa.—Rugal folds numerous in longitudinal parallel rows throughout entire length of stomach with infrequent transverse ridges connecting single pairs of rugae; folds in compressed zig-zag configuration throughout stomach; extensive variation in height of rugae but individual folds uniform in height throughout length.

Zone of cardiac mucosa here considered absent as mucous glands at pyloric sphincter and gastroesophageal junction indistinguishable morphologically and histochemically; pyloric mucosa extending 3 to 4 mm laterally from pyloric sphincter to beginning of fundic tube (inclusive of mucosa at cardiac junction); transitional zone narrow, symmetrical, occupying proximal-most 3.0 mm of fundic tube; remaining 95% of stomach lined with markedly reduced fundic mucosa unlike any other bat examined; gastric mucosa deepest within pyloric zone where glands truly tubular, decreasing progressively through pylo-fundic transition to shallow acinar glands of fundic tube.

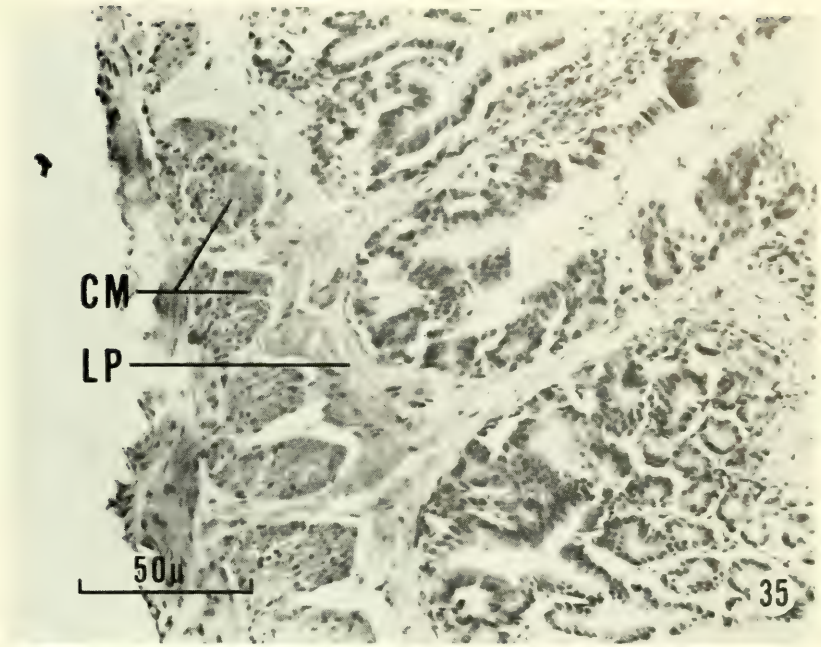
Cardiac glands.—Considered absent as mucous glands at gastroesophageal junction broad, relatively straight and tubular, indistinguishable from those at pyloric sphincter.

Fundus.—Fundic-type mucosa occupying nearly all of inner lining to apex of caecum; uniformly shallow throughout; expression "tubuloacinar" as applied to fundic glands by Rouk (1968) appropriate; glands pouched, short and broad (Fig. 36); simple branched tubular glands characteristic of mammalian fundic mucosa not observed. Depth of fundic mucosa 60 to 70.

Chief cells normally within basal third of gland, maximally to midpoint; cells pyramidal, narrow and elongate; nuclei small, rounded, and always located basally. Argentaffin cells present although extremely rare; more or less triangular, broader than those of other species examined; nucleus small and ovoid; peripheral granulation not observed.

Parietal cells not abundant, sparsely distributed from base (occurring among chief cells) to gastric pit; uniformly large and usually circular; not abundant enough to allow examination of intraglandular size gradient although no small parietal cells observed; nuclei greater in diameter than those of adjacent mucous neck cells and uniformly circular.

Mucous neck cells most abundant element; cells small, more or less cuboidal, with small antero-posteriorly compressed nuclei; cells extending throughout middle 30-50% of gland. Gastric pits necessarily short and



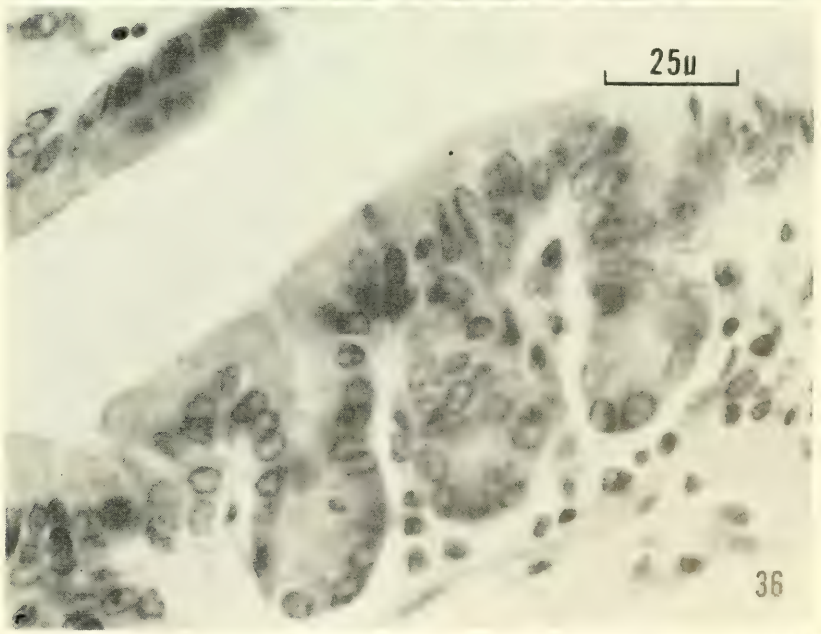


FIG. 35. Stomach wall of *Desmodus rotundus* (lower fundus) showing lamina propria (LP) and circular muscle (CM); note the tubuloacinar-type mucosal glands, extensive lamina propria, and bundling of circular fibers.

FIG. 36. Tubuloacinar fundic glands of *Desmodus rotundus*. The longitudinal axis of the stomach is left to right.

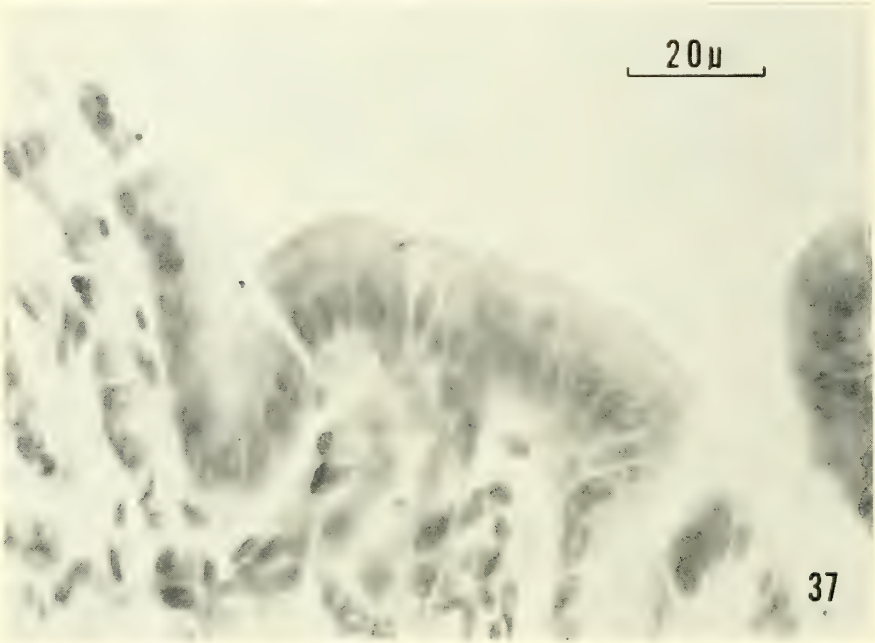


FIG. 37. Surface epithelium of fundic mucosa in the stomach of *Desmodus rotundus*.

sometimes simple pore within surface epithelium; distinctive and rather broad lumen throughout length of gland. Surface epithelium extremely thick (Fig. 37) throughout all fundic mucosa; cells narrow and elongate, with small slightly ovoid nuclei within basal third of cell, extensive mucous border along lumenal surface. Lamina propria extensive beneath and between fundic glands, collagenous fibers infrequent, however.

Pylo-fundic transition zone.—Occupying narrow band within uppermost portion of tubular stomach immediately to left of gastroesophageal junction; acquisition of zymogenic cells abrupt at terminal margin; definition of initial onset of sparse parietal cells difficult, although cells appear immediately within glands and are notably reduced in depth (latter character signifying beginning of transitional zone in this bat); reduction in glandular depth at initial margin fairly abrupt, most of transitional area composed of tubuloacinar elements; gastric pits also decreasing abruptly in depth; lamina propria consistent with that of fundus; depth of transitional glands 70 to 150.

Pyloric glands.—Originating at gastroesophageal junction and extending aborally to distal edge of pyloric sphincter and laterally to initiation of caecal tube; short, broad, tubular glands composed of single cell type; not notably coiled, broadly expanded at base, slightly expanded at upper limit. Cells narrow and elongate, numerous in cross-section of tubule; nuclei

small, spherical, located basally. Lumen extremely broad in base of gland, narrowing only slightly toward upper exit; glands deepest and narrowest at cardiac junction, shallowest at onset of oxynctic mucosa and at pyloric sphincter. Surrounding lamina propria and smooth muscle fibers considerably less abundant than within transitional or fundic mucosa. Depth of pyloric mucosa 150 to 210.

Glands of Brunner.—Restricted to proximal 2.5 mm of duodenum and totally submucosal; distributional pattern similar to that in several other bats examined; pronounced external constriction at pyloric sphincter resulting from lateral expansion or bulge of glandular mass at proximal end of duodenum; glands similar dimensionally and morphologically to those of *Artibeus;* tubules broad, typically highly coiled; cells relatively numerous; nuclei slightly smaller and more nearly ovoid than those of *Artibeus;* lumen broad, increasing slightly in breadth toward crypts of Lieberkühn; lamina propria mucosae and smooth muscle fibers of muscularis mucosae most extensive between tubules among bats examined.

Remarks.—Several authors including Huxley (1865), Grassé (1955), Schultz (1965), and Rouk (1968) have previously illustrated and briefly discussed the topography and gross morphology of the stomach of *Desmodus.* Additionally, Schultz illustrated the gastroesophageal and pyloric areas of a closely related species of vampire, *Diphylla ecaudata.* Grossly, the stomach of *Diphylla* differs from that of *Desmodus* primarily in having a more laterally-displaced pyloric sphincter relative to the gastroesophageal junction (after Schultz), with a resulting probable increase in the distribution of pyloric mucosa. Robin (1881) noted that the caecum of *Diphylla* averages somewhat shorter than that of *Desmodus.* Of the previous investigators, only Rouk has endeavored to describe the composition of the gastric mucosa; my account differs somewhat in content from his.

The elongate tubular stomach and the tubuloacinar-type mucosal glands are unique among bats examined. Because partly or wholly digested food materials that are present in the plasma of the ingested blood meal may represent the essential food source of vampire bats, it is not surprising to find a secondary reduction of mucosal cellular elements responsible for secretion of materials active in digestion of albumunous foods. Nutritional elements utilized by vampires and the mechanisms of intestinal absorption are little understood, thus retarding complete evaluation of this striking reduction of gastric mucosa.

Pronounced segregation of circular muscle fibers into loosely arranged bundles, with prominent amounts of interposed loose connective tissue, probably permits adequate stretching of the caecal wall to allow ingestion of rather large blood meals (see Wimsatt and Guerriere, 1962). Additionally, these authors noted an extensive condensation of the blood meal in the

stomach, with copious urine excretion following ingestion. The extensive vascularization of the stomach observed in *Desmodus* accounts morphologically for the rapid and distinctive fluid absorption from the stomach of this species.

Family NATALIDAE

Natalus stramineus Gray, 1838

Specimens examined (1).—One specimen from Nicaragua of *Natalus stramineus saturatus* (KU 106280).

Overall dimensions.—Greatest length 7.3; greatest breadth 3.2; gastroesophageal junction to pyloric sphincter 3.9; gastroesophageal junction to apex of fundic caecum 3.3; breadth pylorus at sphincter 0.9.

General morphology.—Stomach small, markedly comma-shaped; generally similar to stomach of *Plecotus* in gross morphology, but strikingly like stomach of soricids described by Myrcha (1967); fundic caecum moderate in size, not directed anteriorly (but laterally), apex narrowly rounded with no partitioning of caecum by folds of musculature. Well-developed cardiac vestibule (Fig. 38) formed partially of dilated lower terminal end of esophagus (Fig. 39), hence uppermost portion of vestibule lined with stratified squamous epithelium (unique among bats examined); esophagus entering stomach directly anteriorly, hence no angle of entrance and no incisura cardiaca; cardiac vestibule grades gently into lesser curvature; junction with stratified squamous epithelium abrupt and inferior to dilation of terminal end of esophagus, cardiac orifice thus extremely broad; stratified squamous epithelium smooth at junction with gastric mucosa; no evidence of active cardiac sphincter.

Tubular stomach distal to cardiac junction long and narrow; musculature as well as pyloric sphincter better developed on greater than on lesser curvature; pronounced sulcus intermedius proximal to pyloric sphincter; stomach only slightly curved on the whole, tubular region relatively straight as compared to other bats examined and lying in plane nearly perpendicular to plane of esophagus; slight antero-lateral inflection of terminus originating at sulcus intermedius. Marked external constriction at pyloric sphincter; sphincter includes muscularis mucosae and circular layer; sphincter longer and narrower on greater curvature. Lamina propria well represented beneath muscularis mucosae in rugae, otherwise scant, never abundant above muscularis mucosae layers.

Mucosal folds well developed throughout stomach; musculature substantially thicker in greater than lesser curvature.

Musculature.—Stomach wall extremely thin throughout lesser curvature from apical arc of fundic caecum to just proximal to pyloric sphincter. Oblique muscle layer (muscularis mucosae) unusually thick and dense in midregion between gastroesophageal junction and pyloric sphincter on

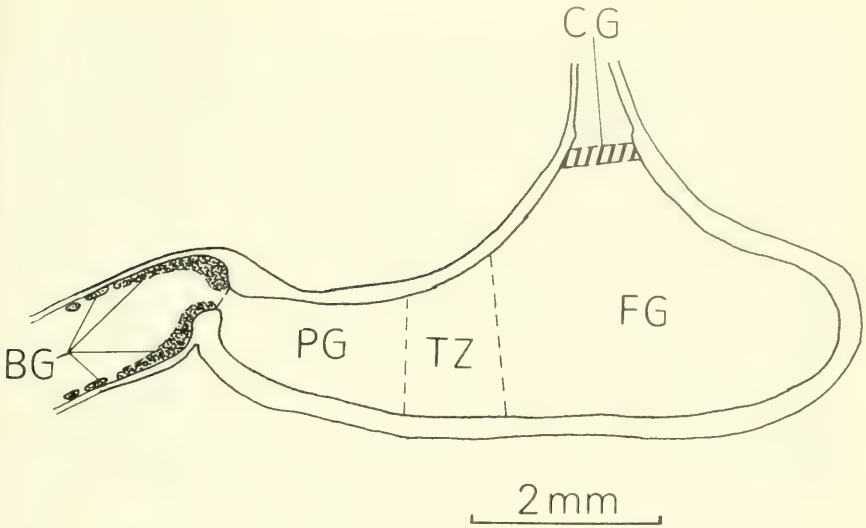
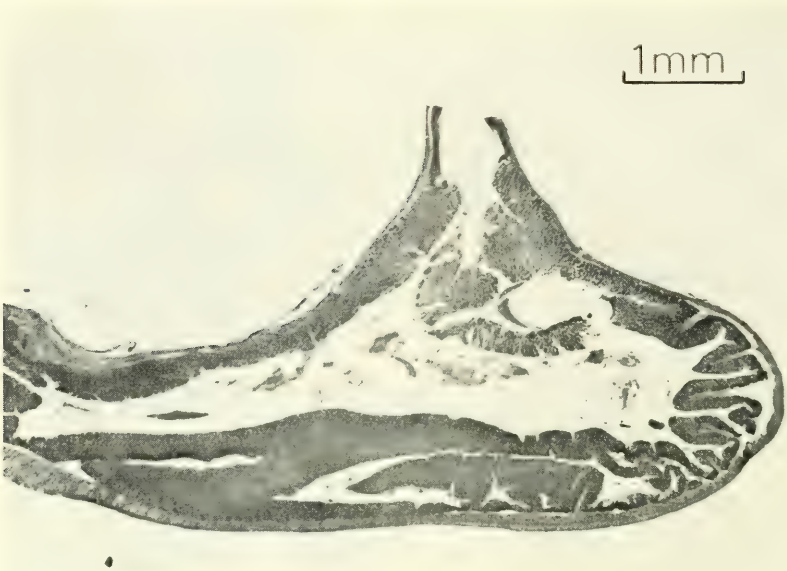


Fig. 38. Mid-longitudinal representation of the stomach of *Natalus stramineus*. For explanation of symbols, see Figure 3.

lesser curvature, at one point as thick as circular and longitudinal layer combined, formed of typically thin sheets throughout remainder of stomach. Sheets of muscularis mucosae within esophagus continuous with those of stomach with no alteration of morphology. Musculature (externa) of apex and lower surface of fundic caecum three times thickness of that of lesser curvature wall; longitudinal layer as deep as circular layer in much of fundic caecum. Circular muscle layer of greater curvature deep throughout, with some "bundling" in area adjacent to fundic caecum; longitudinal layer shallow; marked local thickening of circular muscle layer just proximal to pyloric sphincter (only within greater curvature). Depth longitudinal layer 10 (lesser curvature) to 45, circular layer 30 to 140, muscularis mucosae 4 to 15 (lesser curvature).

Organization of the gastric mucosa.—Mucosa gathered uniformly into parallel, longitudinal rows throughout all of stomach with no interdigitation of ridges; mucosa deepest along lesser curvature especially in midregion at base of cardiac vestibule; only slightly reduced in depth at apex of fundic caecum and considerably less so than in *Plecotus* with no reduction in frequency of rugae at apex; pyloric mucosa deep (deeper than most of fundic complement); fundic mucosa deep at junction with esophagus, uniform in depth throughout most of cardiac vestibule (in contrast to shallow, variable cardial mucosa of *Plecotus*); cardiac glands unusual in both morphology and distribution (found beneath esophageal epithelium at cardiac junction as well as in stomach proper); fundic mucosa [illegible]



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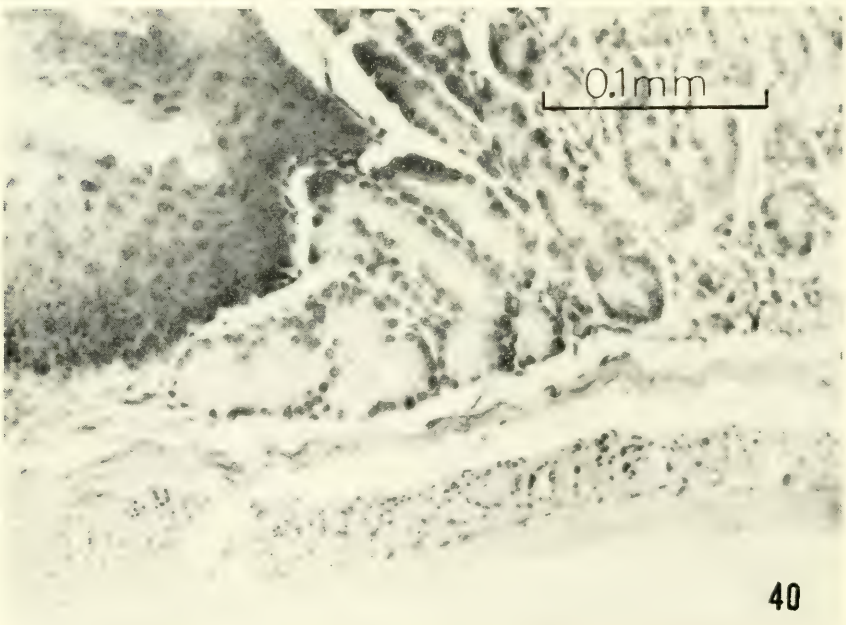

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FIG. 39. Photograph showing cardiac vestibule of *Natalus stramineus*. Note the narrow wall of the lesser curvature in contrast to the greater curvature.

FIG. 40. Large cardiac glands at the gastroesophageal junction of *Natalus stramineus*.

most of internal surface area of stomach (as in other bats) but unusual in being most highly developed within fundic caecum; pylo-fundic transition zone extensive as zymogenic cells limited in distribution; pyloric mucosa well represented and more extensive in distribution than most species examined.

Glands of Brunner relatively sparse, present in small noncontinuous clumps in proximal 3 mm of duodenum and superior surface of pyloric sphincter.

Cardiac glands.—Small band of highly convoluted tubular glands adjacent to, and beneath, lower limit of stratified squamous epithelium at gastroesophageal junction; mostly superior to muscularis mucosae but found also between the two layers of this tissue in uppermost area of distribution under esophageal lining. Glands extremely large (Fig. 40), two to three times breadth of adjacent gastric glands; lumen extremely broad, superior-most glands appear to empty through pits formed of modified stratified squamous epithelium; glands composed of single cell type indistinguishable in morphology and staining reactivity (refer to section on histochemistry of cardiac glands) from cells of glands of Brunner; cardial cells large and with extensive mucous border; nuclei small, spherical, juxtaposed to basement membranes; cytoplasm agranular and stains extremely pale pink with eosin Y; connective tissue not abundant but more so than that observed between glands of fundus; transitional glands between cardiac and fundic mucosa difficult to identify, at best an extremely narrow zone characterized by occasional parietal cell in base of gland. Depth of cardiac glands 100.

Fundus.—Extensive variation in depth and complements of cellular elements; true fundic glands best developed within fundic caecum and along lesser curvature near gastroesophageal junction; extensive variation in depth with deepest glands along (1) upper wall of fundic caecum, (2) within cardiac vestibule, and (3) at apexes of rugal folds; fundic mucosa slightly reduced in depth at extreme apex of fundic caecum with marked reduction in furrows between adjacent fundus 95 to 230.

Zymogenic cells in highest concentration within, and in areas immediately adjacent to fundic caecum; occupy lower 50% of gland in most areas, some areas of fundus with chief cells in lower 20% of gland (throughout much of greater curvature); chief cells gradually reduced in numbers lateral to plane of gastrosophageal junction in direction of pylorus; cells pyramidal to trapezoidal or polyhedral, with large, basal, spherical nuclei; basal region of gland including chief cells bulbous, parietal cells not common among chief cells. Argentaffin cells positively identified as occurring among basal-most cells; morphology essentially that as described by Schu

field (1953) for argentaffin cells of human small intestine; cells long and narrow with nucleus displaced medially; dense peripheral granulation.

Parietal cells abundant throughout most of fundus and transitional area; notably abundant in upper portion of glands resulting in extremely shallow gastric pits; cells circular to ovoid in lower areas of gland, becoming smaller and more rounded in upper portions of tubules; parietal cells reduced substantially in frequency throughout apical arc of fundic caecum accounting for slight reduction in glandular height.

Mucous neck cells typically small with unusually large nuclei; occur in small, tightly compressed clumps wedged among adjacent parietal cells; little cytoplasm. Gastric pits extremely shallow throughout all of fundus as well as transitional areas; pits rarely more than fifth total length of gland, even in fundic caecum; parietal cells occasionally found just beneath surface epithelium suggesting essential absence of gastric pit and presence of simple "pore"; cells lining pits having typically large nuclei of lower mucous neck cells, nuclei becoming slightly laterally flattened toward surface of mucosa. All mucous cell components of glands of fundic caecum have more spherical nuclei than found in remainder of fundus. Surface epithelium thick; nuclei large, basal, club-shaped; cells in single layer. Connective tissue beneath glands nearly absent, glands often resting on muscularis mucosae.

Pylo-fundic transition zone.—Region extensive owing to relatively limited distribution of zymogenic cells as discussed previously; glands exceptionally narrow and long, parietal cells abundant throughout most of length; parietal cells sometimes in continuous column within glands and in substantially greater numbers than mucous neck cells; loss of zymogenic cells at beginning of zone gradual; loss of parietal cells at terminus of area also gradual with one or a few cells persisting in proximal-most pyloric glands; gastric pits as shallow as those of fundus proper; surface epithelium unchanged over that of fundus; little or no progressive decrease in depth except for slight decrease at point where parietal cells finally disappear; depth 180 to 220.

Pyloric glands.—Zone of pyloric glands relatively extensive in comparison to total internal surface area of stomach, best developed on lesser curvature; glands generally narrow at origin of distribution, increasing in breadth toward termination at onset of glands of Brunner in duodenum. Glands composed of single cell type in single layer; nuclei large and spherical throughout. Gastric pits deep to base of gland (as characteristic of pyloric glands, mucous border of glands narrow resulting in broad glandular lumen; cells considerably larger than mucous neck cells of fundic glands; surface epithelium deeper than that of fundus owing to much larger epithelial cells; glands terminate at beginning of Brunner's glands on distal surface of

pyloric sphincter. Lamina propria more abundant at base of, and between, pyloric glands than in fundic mucosa. Depth of pyloric mucosa 200 to 230.

Glands of Brunner.—Occur in discontinuous patches beneath muscularis mucosae in proximal 3 mm of duodenum; ring of glands occupy entire distal surface of pyloric sphincter, decreasing gradually in abundance to terminate 0.5 mm from sphincter; other smaller patches of three to six glands occur distal to main group; proximal-most glands extremely large with spherical and peripheral nuclei and extensive cytoplasmic complement; more distal isolated clumps considerably smaller and nuclei always small and markedly flattened, lumen much narrower. Cells and glands indistinguishable from previously described "cardiac" glands. Brunner's glands clearly different in both distribution and morphology from other bats examined.

Remarks.—The stomach of *Natalus stramineus* is unique among bats examined (and notably similar to stomachs of soricid insectivores studied by Myrcha, 1967) in possessing a terminal pyloric section oriented nearly directly laterally with little recurvature craniad. Also, *N. stramineus* possesses the largest and most distinctive cardiac vestibule among carnivorous bats studied.

The cardiac gland zone, although typically narrow, is distinctive in several respects. These glands are highly convoluted and extremely broad, a combination of features observed only in *Natalus*. Several tubules were observed to open through pores within the squamous epithelium at the gastroesophageal junction; thus, the cardiac glands lie partially beneath esophageal epithelium. Additionally, tubules of cardiac glands in cross-section are nearly indistinguishable from the glands of Brunner of the same bat. Bensley (1905) and others have noted unusual similarity between cardiac glands and Brunner's glands in several species of mammals, although the present case appears to be the first reported for bats. In all other species examined, the two glandular types were clearly distinctive in morphology within each bat.

The fundic mucosa resembles most closely, among bats examined, that of *Plecotus* in distributions and morphology of cellular components, as well as in pattern of mucosal reduction in the fundic caecum. *Natalus* and *Plecotus* differ, however, in distribution of different mucosal elements; the pyloric zone is more extensive in *Natalus*, shifting the transitional area medially, thus reducing the extent of the fundic mucosa relative to that observed in *Plecotus*. Additional specimens of *Natalus* must be studied in order to verify the tentative conclusions presented here.

Family VESPERTILIONIDAE

Plecotus townsendii Cooper, 1837

Specimens examined (3).—Three specimens of *Plecotus townsendii pallescens* from South Dakota.

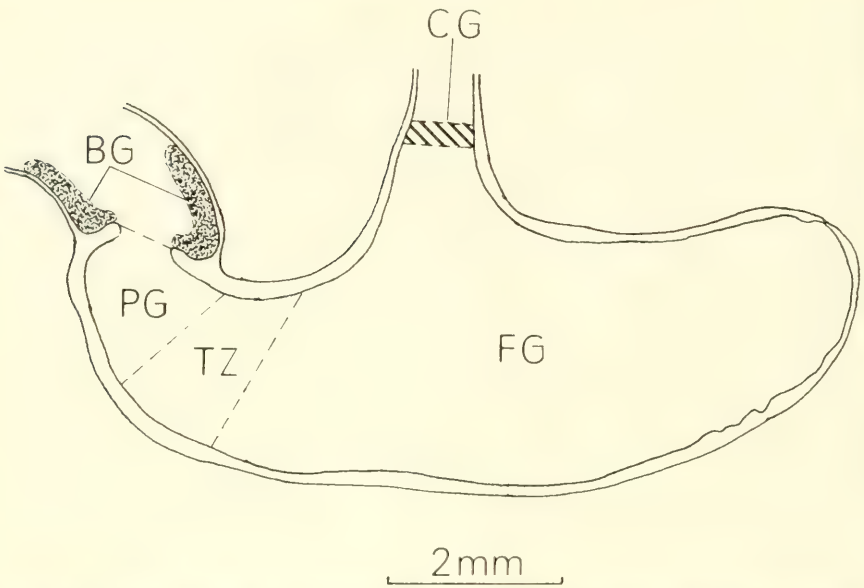


FIG. 41. Mid-longitudinal representation of the stomach of *Plecotus townsendii*. For explanation of symbols, see Figure 3.

Overall dimensions.—Greatest length 8.9-9.5; greatest breadth 3.1-3.8 (inclusive of cardiac vestibule); gastroesophageal junction to pyloric sphincter 2.5-2.7; gastroesophageal junction to apex of fundic caecum 4.6-5.1; breadth pylorus at sphincter 2.0-2.1.

General morphology.—Stomach saccular and reniform (when empty), notably symmetrical with cardiac vestibule at midpoint of lesser curvature (Fig. 41); caecum extensive but unpouched, occupying nearly half length of stomach; apex of caecum relatively blunt and directed antero-laterad, upper limit of caecum lying approximately in same plane as pyloric sphincter and posterior limit of cardiac vestibule; caecum unusual in being long, rather pointed, directed somewhat craniad, and extending a distance equal to, or greater than, tubular stomach distal to cardiac junction; cardiac vestibule moderate in height, expanding gradually into lesser curvature; distance from esophageal junction to apex of fundic caecum greater than that to pyloric sphincter; junction having stratified squamous epithelium of esophagus abrupt, no suggestion of active muscular cardiac sphincter; incisura cardiaca absent (esophagus entering stomach perpendicularly). Terminal stomach distal to esophageal junction relatively short and broad; musculature of pyloric sphincter (Fig. 42) relatively uniform in mass throughout, but slightly more massive on greater than on lesser curvature, thicker along luminal edge than elsewhere; musculature of sphincter composed exclusively of inner circular layer plus thin sheets of muscularis

mucosae that line sphincter mass; notable external constriction circumscribing pyloric sphincter; glands of Brunner moderate in abundance and restricted to distal surface of pyloric valve musculature and proximal-most 2 mm of duodenum. Esophageal junction in a plane distinctly anterior to that of pyloric junction owing to moderately well-developed cardiac vestibule (Fig. 41); cardiac vestibule and pyloric orifices directed in approximately same direction, terminal stomach at nearly right angle to plane of remaining stomach; stomach generalized in gross morphology with little apparent specialization of structure.

Musculature.—Muscle layers generally moderate in depth when compared to other bats examined; total muscularis externa slightly thicker within lesser than greater curvature, circular layer notably thickened in terminal half of pyloric tube (especially thick in greater curvature); circular muscle layer always substantially thicker than longitudinal layer except in extreme apical tip of fundic caecum where layers approximately equal in depth; ganglia of Auerbach's plexus rare; extensive bundling of circular muscle occurs throughout proximal two-thirds of greater curvature; no suggestion of a muscular cardiac sphincter; depth longitudinal layer 15 to 25, circular layer 40 (caecum) to 160 (pyloric tube), muscularis mucosae less than 10 to 15.

Organization of gastric mucosa.—Mucosa clearly gathered longitudinally throughout sides of stomach (dorsal and ventral surfaces of organ *in situ*); rugal folds exceptionally numerous, long, narrow, and notably high; folds gathered uniformly longitudinally throughout all of terminal portion; folds clearly oriented transversely at apex of fundic caecum (Fig. 43) and within greater curvature up to onset of terminal stomach, and occurring as deep "pyramids" of mucosa lying directly along arc of greater curvature and wall of fundic caecum; folds of cardiac vestibule directed longitudinally; folds greatest in breadth in pyloric tube, decreasing gradually in breadth toward apex of caecum; folds of fairly uniform depth throughout sides, zig-zag orientation in lower half of caecum (Fig. 44), notably deeper along arc of greater curvature; slight increase in depth of folds in lesser curvature; substantial reduction in gastric mucosa only in apex of fundic caecum where folds are short, narrow, and relatively sparsely distributed; folds along arc of greater curvature in unusual configurations (extremely long, narrow "fingers" often expanded at their apexes) (Fig. 43).

Well-defined cardiac, fundic, and pyloric glands present; cardiac zone extremely narrow (one or two glands in breadth); pyloric zone relatively narrow; fundo-pyloric transition area relatively broad as transition to pyloric gland mucosa is gradual; fundic mucosa occurring throughout saccular stomach and cardiac vestibule.

Cardiac glands.—Junction with stratified squamous epithelium abrupt;

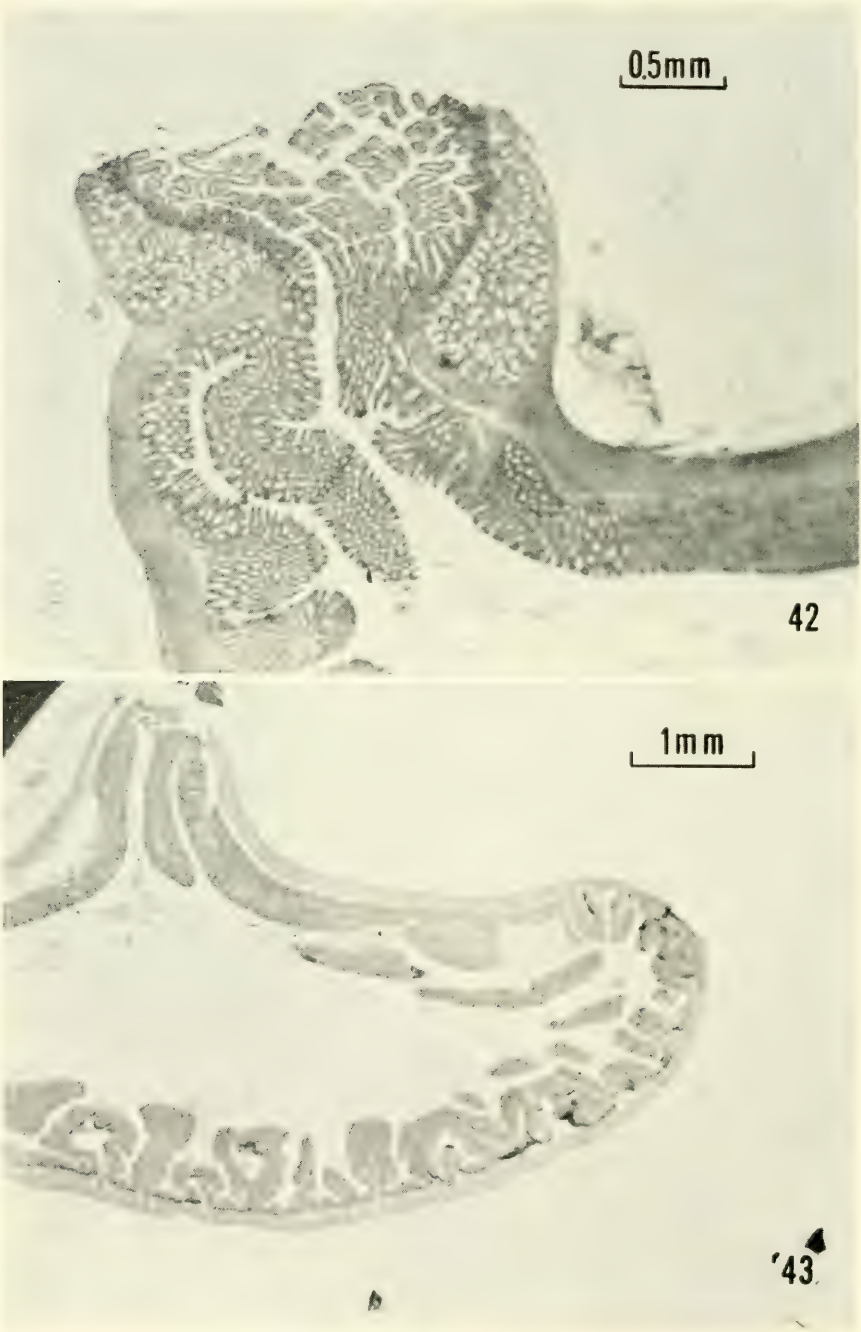


FIG. 42. Pylo-duodenal junction of *Plecotus townsendii*.

FIG. 43. Mid-longitudinal section of stomach of *Plecotus townsendii* showing short, broad, rugal folds of greater curvature.

glands long and narrow, with extremely limited distribution, composed of single cell type; mucous cells of somewhat variable morphology throughout gland as basal cells of lower third of tubule small, compact, rectangular, more numerous than upper cells and with nuclei peripheral and spherical; cells of upper two-thirds with progressively more laterally flattened nuclei and cells more elongate than in basal elements; gastric pits always broad and increase in breadth toward luminal surface; glands increase slightly in depth from cardiac junction to transitional fundic zone. Transitional zone from cardiac to fundic mucosa narrow with infrequent parietal cells in lower half; gastric pits relatively deep until onset of true fundic glands. Depth of cardiac glands 200 to 300, breadth of cardiac zone 60 to 100.

Fundus.—Glands relatively short and broad throughout most of fundus, long and narrow only on lesser curvature within (and lateral to) cardiac vestibule; fundic mucosa best developed on lesser curvature but notably reduced within extreme apex of fundic caecum; all cellular components large and relatively few in number. Depth of fundic glands 80 to 180.

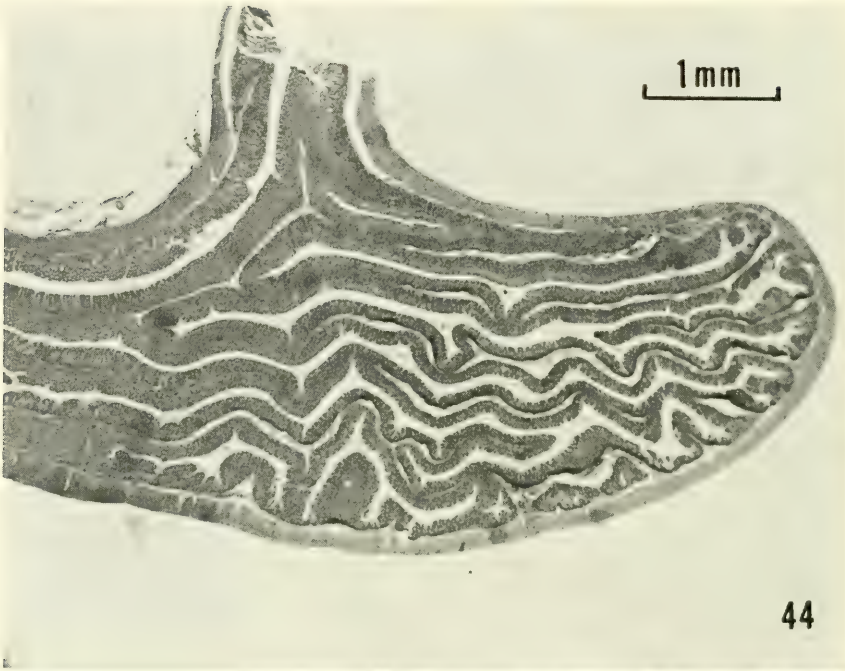
Basal zymogenic cells large, pyramidal with spherical nuclei; may occupy up to 60% length of gland but usually about 40%; cells rather uniform in size throughout stomach and reduced in size and number only in apex of elastic stomach; chief cells form basal "bulbous" expansion of gastric gland.

Parietal cells relatively large and usually spherical (but occasionally ovoid) with large, spherical nuclei centrally located in cell; greatest density of cells in medial half of gland occurring extremely infrequently among chief cells and most often in clumps of three or four but occasionally as many as 20; marked increase in cell size from bottom to top of distribution (uppermost cells extremely large), whereas nuclear size remains constant; only marked decrease in numbers in terminal half of fundic caecum (with corresponding increase in cell size), slight increase in relative numbers in pylo-fundic transition area; intercellular canaliculi pronounced.

Mucous neck cells interspersed singly or in small clumps among parietal cells and most common just above chief cells (where parietal cells less numerous) and, of course, in necks of gastric pits; little if any size variation within gland; nuclei spherical, slightly smaller than those of parietal cells.

Argentaffin cells extremely rare in base among chief cells; small and with peripherally located granulation but otherwise clear cytoplasm; not observed elsewhere in stomach.

Gastric pits relatively deep; mucous pit cells large with spherical nuclei which become slightly flattened laterally in upper portion of pit; cells usually occupy 40-50% length of gland and occasionally three-fourths its length. Surface epithelium thick; nuclei extremely large and ovoid, often "club-shaped."



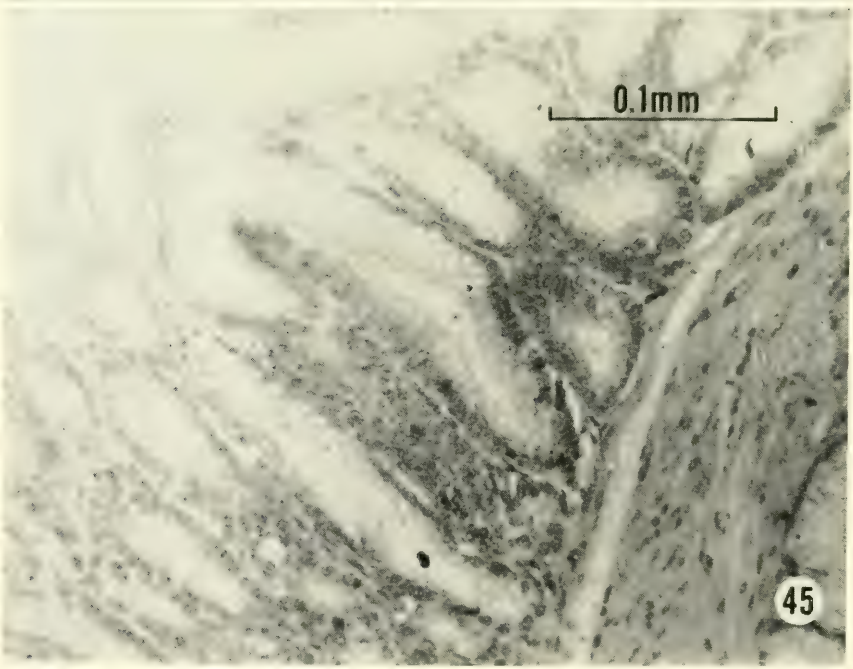


FIG. 44. A longitudinal section showing mucosal folds (rugae) in stomach of *Plecotus townsendii*.

FIG. 45. Pyloric glands of *Plecotus townsendii*.

Pylo-fundic transition zone.—Transition to pyloric glands gradual and zone relatively broad; abrupt loss of zymogenic cells, whereas parietal cells reduced in numbers only gradually, those remaining in terminal portion of transition large; mucous cells increase in frequency as parietal cells reduced; no change in glandular depth over that of fundus; transition zone occupies approximately angular portion of stomach; depth 120 to 170.

Pyloric glands.—Extremely broad and massive (Fig. 45), each gland expanded into giant bulb at base; lamina propria between adjacent glands substantially better developed than in fundic glands with smooth muscle fibers extending between glands within lower half of layer; extensive variation in nuclear shape between glands, nuclei spherical, nuclear structure usually consistent within a given gland; single cell type present with exception of occasional argentaffin cell in extreme base; surface epithelium identical to that of fundus. Glands near pyloric sphincter with narrow, sharply-compressed cells resulting in extremely broad openings of gastric pits into lumen, hence surface epithelium reduced to narrow "clumps." Glands terminate abruptly at distal edge of pyloric sphincter; pyloric glands in relatively narrow zone substantially distal to pyloric bend. Depth of pyloric mucosa 100 to 230.

Glands of Brunner.—Moderate in abundance and in single solid mass on entire distal surface of pyloric sphincter and proximal 1.5 mm of duodenum; highly convoluted, large with broad lumen; cells long, narrow; nuclei extremely small, markedly flattened, and always positioned against basal surface (peripheral); cellular morphology uniform throughout gland; glands always submucosal and restricted to duodenum; muscle fibers of muscularis mucosae prominent between glands; open luminally between crypts of Liberkühn.

Remarks.—The stomach of *Plecotus townsendii* is generalized in gross morphology, being symmetrical in shape, and having a simple fundic caecum and gradual curvature throughout. These features along with distribution of zones of gastric mucosa are similar to those reported for several species of Insectivora by Myrcha (1967), particularly several species of Old World talpids and erinaceids. The pyloric and pylo-fundic transition zones are well defined and approximately equal in length. The contributing muscle layers in the stomach wall are relatively thick with increasing thickness in both upper and lower walls of the pyloric tube toward the pyloric sphincter.

Rouk (1968) described the stomachs of *Myotis velifer* and *Antrozous pallidus* as being of the "simple type," and his figure of the stomach of *Myotis velifer* bears striking similarity to that of *P. townsendii*. It differs slightly in orientation of the cardiac vestibule and in distribution of pylo-fundic transitional mucosa. All three genera (*Antrozous*, *Myotis*, *Plecotus*)

have more or less symmetrical stomachs with a fundic caecum hooked craniad, smooth overall curvature, a gradual (rather smooth) pyloric bend, a moderately thick pyloric sphincter, and a short, narrow cardiac vestibule.

A photograph published by Fischer (1909:124) of a "Situspräparat der Baucheingegeweide von *Plecotus auritus*" showed the stomach of this species to be virtually identical topographically to that described here for *P. townsendii*.

Pizonyx vivesi (Menegaux, 1901)

Specimens examined (1).—One specimen from Isla Partida, Gulf of California (KU 113998).

Overall dimensions.—Greatest length 10.0; greatest breadth 7.1; gastroesophageal junction to pyloric sphincter 1.8; gastroesophageal junction to apex of fundic caecum 6.0; breadth pylorus at sphincter 2.6.

General morphology.—Stomach large and generally tubular but extremely rounded through fundic caecum and greater curvature (Fig. 46); expanded substantially in antero-posterior direction; dorsal surface convex; pyloric tube short.

Cardiac vestibule short and, although cardiac glands comparatively abundant within vestibule, thick-walled and extremely narrow in relation to breadth of pylorus; vestibule increasing gradually and slightly in breadth from gastroesophageal junction to incorporation into lesser curvature, situated approximately midway along lesser curvature; esophagus entering stomach at slight angle to lesser curvature, creating incisura between vestibule and caecum; incisura cardiaca short and broad with muscle layer prominently thickened locally and longitudinal layer unchanged; gastroesophageal junction abrupt with all muscular complements continuous between esophagus and vestibule but with slight local thickening of muscularis mucosae and lamina propria mucosae at junction; no specific evidence of an anatomical sphincter. Gastric orifices in relatively close proximity to each other and generally equivalent in direction anteriorly, although vestibule slightly acute to pyloric tube.

Fundic caecum extremely large and spacious but not truly saccular, gently rounded, nearly spherical; musculature reduced in depth within extreme apical portion of caecum only with no external or internal features suggesting anatomical demarcation from remaining stomach.

Tubular portion at terminal point distal to plane of vestibule more than twice breadth of gastroesophageal junction, directed anteriorly to the right; pyloric curvature gradual and continuous with musculature prominently thickened throughout tubular portion (which tapers little to pyloric sphincter). Musculature of pyloric sphincter short and massive, appearing more or less uniform in depth throughout; sphincter a simple, rounded projection of circular muscle from wall of pylorus, valve displaced more craniad

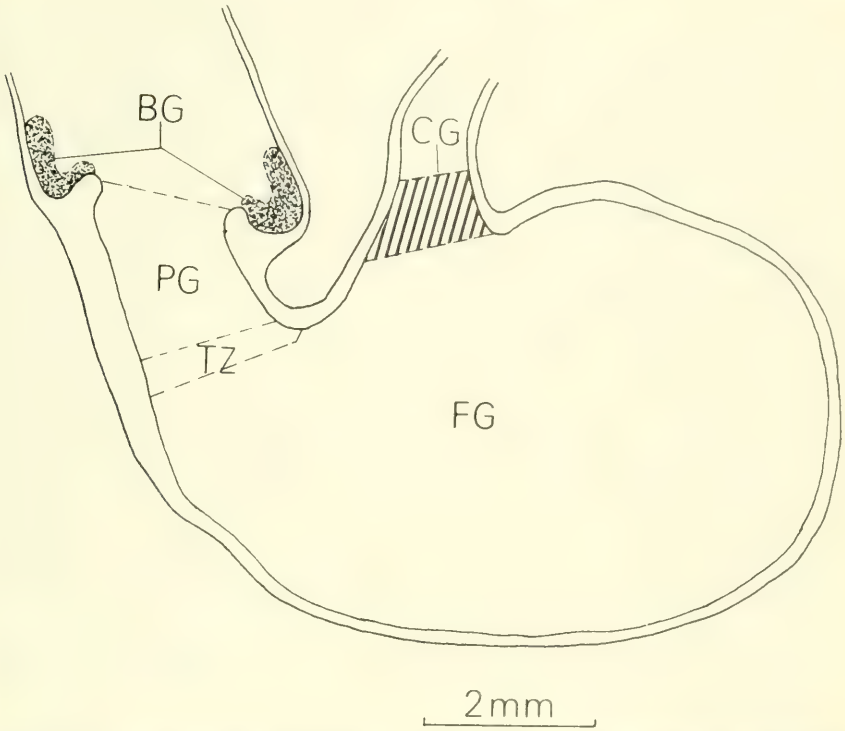


FIG. 46. Mid-longitudinal representation of the stomach of *Pizonyx vivesi*. For explanation of symbols, see Figure 3.

on greater than on lesser curvature; mucosa lining sphincter slightly reduced in depth over that of remaining pylorus; deep but narrow external constriction at pyloric sphincter; glands of Brunner not abundant and restricted to duodenum; sulcus intermedius absent, sulcus angularis present but not pronounced.

Pattern of depth of muscular wall similar to that observed in *Plecotus;* gastric mucosa deep throughout sides and apexes of rugal folds with pattern of local reductions of mucosa similar to that found in *Plecotus;* lamina propria mucosae considerably more prominent than in *Plecotus,* loose lamina with abundant collagenous fibers best developed throughout greater curvature and within rugae (including fundic caecum to apex), much less pronounced through lesser arc; elastic fibers generally infrequent (including fundic caecum) and lamina propria between mucosa and muscularis mucosae typically infrequent throughout.

Musculature.—Longitudinal layer of uniform breadth throughout all of greater curvature and through fundic caecum to just lateral of incisura cardiaca, reduced to thin remnant sheet through incisura cardiaca, [illegible]

vestibule, and all of remaining lesser curvature to pyloric sphincter. Variation in depth of circular layer within stomach basically similar to pattern in *Plecotus;* circular layer differing from that in *Plecotus* in being approximately equal in depth within much of greater and lesser curvatures (consistently deeper in lesser as compared to greater curvature in *Pelcotus*) with proportionally greater thickening within pyloric tube, gathering of circular fibers into transverse bundles more frequent and bundles larger (although restricted to greater curvature and apex of fundic caecum as in *Plecotus*), and in having more extensive inter-bundle complements of lamina propria. Muscularis mucosae uniform in depth throughout stomach wall but notably deeper within rugae. Depth longitudinal layer 15 to 45, circular layer 35 to 250, muscularis mucosae less than 10 to 25.

Organization of gastric mucosae.—Pattern of gathering of mucosal folds notably similar to that of *Plecotus;* folds oriented strictly longitudinally throughout tubular portion, longitudinally directed through dorsal and ventral walls of fundic caecum with pronounced zig-zag orientation within lower one-half of caecum (as in *Plecotus*); short, transversely directed folds originating along greater curvature not nearly so abundant as in *Plecotus,* but transverse folds along lesser curvature of fundic caecum as in *Plecotus.* Rugae numerous, nowhere locally reduced in number; rugal folds comparatively broader and deeper than those of *Plecotus,* probably as function of increased stomach size.

Zones of gastric mucosa well defined with relatively few transitional elements from one major glandular type to another; region of cardiac glands extensive relative to all other bats examined, occupying major portion of short cardiac vestibule; fundic mucosa locally variable in morphology within extensive fundic stomach, lining all of remaining stomach except pyloric tube; transition from fundic to pyloric mucosa relatively abrupt, with zone narrow as compared to *Plecotus* and two other vespertilionids previously examined (Rouk, 1968), confined to narrow area within pyloric curvature; pyloric glands extremely large and prominent, occupying most of tubular stomach distal to pyloric bend. Mucosa consistently deep throughout stomach, reaching greatest depth within pyloric zone; pronounced reduction in depth of glands within furrows of fundic zone only (similar to condition of *Plecotus*), pattern of reduction of mucosal depth on sides and surfaces of rugae within apical arc of fundic caecum similar to pattern in *Plecotus.*

Cardiac glands.—Glands occurring in broad, deep zone 1 mm in length at gastroesophageal junction (Fig. 46); glands extremely broad, being three times breadth of adjacent fundic glands; cells within basal fourth small, elongate and tightly packed within basal arc; nuclei usually peripheral, extremely small, spherical, mucous border narrow; cells within upper three-

fourths becoming progressively more elongate (increase in mucous border) toward surface epithelium (with nuclei unchanged in size although modified to prominently flattened discs located in juxtaposition to basement membrane); lumen always extremely broad, especially within bulbous basal expansion as mucous border of basal cellular framework narrow; glands relatively uniform in breadth superior to basal portion; transitional zone to fundic mucosa a narow belt of two or three cardiac-type glands with infrequent basal parietal cells; areolar connective tissue extensive basal to (and between) glands with large numbers of inclusive collagenous fibers (restricted to cardiac zone); depth increasing slightly from gastroesophageal junction to junction with fundic mucosa; depth of cardiac mucosa 250 to 300.

Fundus.—Extensive variation in morphology and depth of glands; best developed in both depth and complements of cellular elements within lesser curvature; significantly reduced in depth between rugae of greater curvature but only slightly between rugae within all of fundic caecum; reduction in depth usually involving reduced numbers of cells, rarely reduction in dimensions of cellular components; glands usually long and narrow, relatively straight and tubular, distinctively expanded basally, thereafter uniform in breadth to surface epithelium; gastric pits also highly variable in depth and breadth. Depth of fundic mucosa 150 to 280 (lesser curvature).

Zymogenic cells occupying lower 40% of gland throughout lesser curvature (especially abundant within lesser curvature) and most of upper two-thirds of tubular portion of fundus; notably reduced in number throughout glands of lower wall of fundic caecum and midregion of greater curvature, increasing again in number in greater curvature within tubular portion; cells large with small, ovoid nuclei located variably within basal third of cell; areas in which zymogenic cells reduced usually having cells only within lower 10-15% of gland (argentaffin-type cells not observed but assumed present).

Parietal cells most abundant in lesser curvature and cardiac vestibule; most common within upper 60% of gland, but scattered and less frequent among chief cells and moderately abundant through apical arc of fundic caecum (within glands on rugae); reduced in abundance and density on dorsal and ventral surfaces in upper portion of gland throughout all of body of stomach (excluding tubular portion); reduction corresponds to 1) increase in depth of gastric pits, 2) reduction of overall glandular depth, and 3) marked drop in number of chief cells; marked lower to upper level size gradient in parietal cells, ranging from small among basal chief cells to those nearly breadth of tubule just beneath necks of gastric pits; parietal cells averaging large and spherical with relatively small, usually spherical nuclei; intercellular caniculi not observed although assumed present.

Mucous neck cells infrequent among closely packed and numerous parietal cells within upper portions of most fundic glands, but more numerous in midregion where parietal and chief cells less abundant; mucous neck cells identical in morphology to those of *Plecotus* except nuclei small (smaller than those of adjacent parietal cells). Gastric pits varying from 10-25% length of gland throughout lesser curvature to up to 75% within glands of greater arc; increased depth of pits partially attributable to absolute increase in pit depth, as well as relative decrease in glandular depth as compared to lesser curvature; pit cells identical in structure to cells of cardiac and pyloric glands of this species, lumen broad. Surface epithelium approximately two-thirds depth of gastric pit epithelium, cells in tightly packed clumps at interim between adjacent gastric pits; clumps not extensive in mass owing to great breadth of gastric pits; basal lamina propria sparse and with less abundant intertubule matrix than observed in either cardiac or pyloric mucosa.

Pylo-fundic transition zone.—Narrow zone (Fig. 46) illustrating relatively abrupt transition to pyloric mucosa; reduction and subsequent loss of parietal cells fairly abrupt with parietal cells persisting in large numbers throughout nearly all of transitional area; loss of zymogenic cells even more abrupt (within breadth of two or three glands) at initial edge of transitional area; increase in depth of gastric pits gradual from about 30 to 50% length of gland within transitional area, then abrupt increase to base at margin with pyloric mucosa; lamina propria mucosae prominent basally and between adjacent glands and confined in abundance to transitional belt, uncommon in adjacent fundic mucosa; depth 210 to 310.

Pyloric glands.—Occurring within zone equivalent to that of *Plecotus* but notably different in morphology; glands usually large in both length and breadth (Fig. 47), similar to cardiac glands in dimension although slightly broader; cells within basal 10% similar to mucous neck cells, small and with spherical, centrally located nuclei and narrow inner mucous border; remaining 90% of length composed of giant, elongate, columnar cells with small, disc-like, crescent-shaped nuclei and a vast mucous border similar to upper cells of cardiac glands; glands distinctively bulbular at base, narrowed above basal portion, increasing in breadth only slightly to lumenal surface; lumen extremely broad throughout, broadest within basal region; pyloric mucosa restricted aborally to proximal surface of pyloric sphincter, not extending into duodenal lumen; lamina propria especially pronounced between glands, moderate basally. Pyloric, along with cardiac, glands representing most massive single mucosal-type glands observed in entire study. Depth of pyloric glands 250 to 340.

Glands of Brunner.—Not abundantly distributed, occurring in narrow band within proximal 1.1 mm of duodenum and along distal surface of

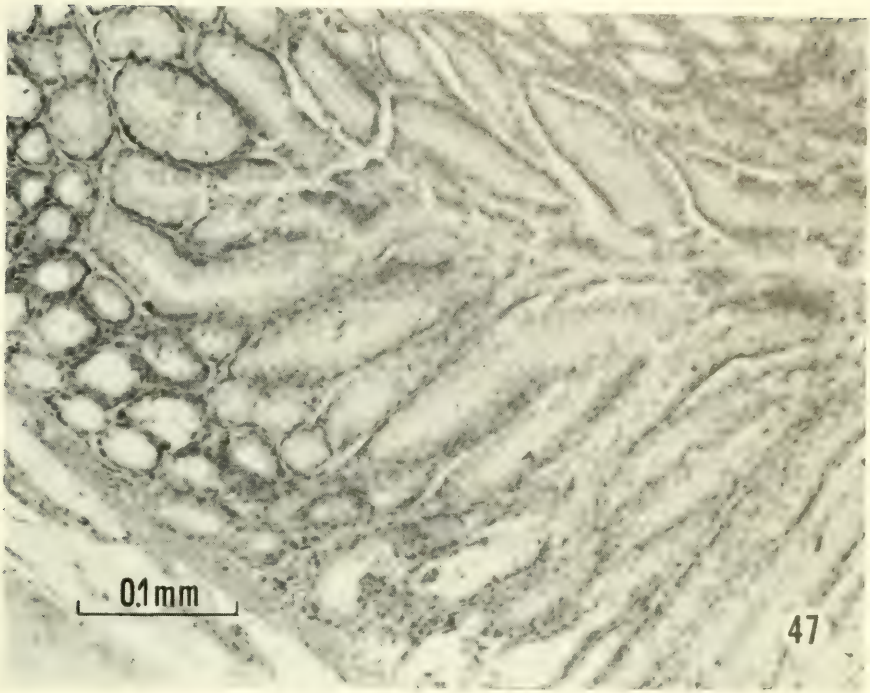


FIG. 47. Pyloric glands of *Pizonyx vivesi*.

sphincter; always submucosal and restricted to duodenum; typically convoluted, uniform in breadth and relatively narrow; cross-sectional structure similar to that found in other bats examined, differing from *Plecotus* only in location and structure of nuclei; nuclei peripheral in cell (but not basal), compressed ovals (usually markedly compressed in *Plecotus*); tubules more heavily enclosed by surrounding smooth muscle fibers originating from muscularis mucosae than in other bats examined; exit from lumen narrow.

Remarks.—The stomach of *Pizonyx* appears to be slightly altered from the basic insectivorous type. The general outline or configuration is similar to that of *Plecotus* and *Rhynchonycteris*, although the stomach of *Pizonyx* is considerably more rounded and has a shorter and broader terminal portion than in either of the other two latter bats. The spaciousness of the fundic portion suggests a modification to assimilate large quantities of food at a single feeding. A noteworthy feature is the extensive distribution of cardiac glands at the gastroesophageal junction. These glands are large, relatively straight tubular, and strikingly similar in morphology to the pyloric glands.

The structure and local variation in depth of the tunica muscularis externa closely resembles that observed in *Plecotus*, although complement-

of loose lamina propria within the muscularis externa and superior to the muscularis mucosae are substantially greater in *Pizonyx*. Although the valves of the pyloric sphincter of *Plecotus* are longer than those of the single specimen of *Pizonyx* examined, the asymmetrical orientation of the flaps is identical in the two species.

Both the pylo-fundic transitional glands and the glands of Brunner are distinctively reduced in distribution as compared to *Plecotus*. Perhaps the narrow transitional zone is a consequence of advancement distally of basal zymogenic cells.

The only feature in which *Pizonyx* clearly resembles *Noctilio leporinus*, another fish-catching bat (of which the stomach was observed macroscopically only), is in the short, broad, gently arched terminal stomach, and this feature is shared also with *Pteronotus parnellii*.

Family MOLOSSIDAE

Molossus ater E. Geoffroy-St. Hilaire, 1805

Specimens examined (2).—Two specimens from Nicaragua of *Molossus ater nigricans* (KU 106285, 106287).

Overall dimensions.—Greatest length 12.1-13.7; greatest breadth 4.1-4.5; gastroesophageal junction to apex of fundic caecum 4.2-4.4; breadth of pylorus at sphincter 1.3-1.4.

General morphology.—Stomach tubular with relatively short, narrowly rounded fundic caecum; generally slight anterior flexure of the stomach resulting in slight convexity of greater curvature; pyloric and cardiac orifices oriented so that pyloric sphincter substantially inferior to cardiac sphincter in stomach *in situ;* terminal portion tapers gradually to pyloric sphincter. Incisura cardiaca present but not well developed, esophagus entering stomach at angle; stratified squamous epithelium extending posteriorly to lesser curvature.

Stomach extensive distal to cardiac junction (see Fig. 48); marked pyloric bend just proximal to pyloric sphincter, endpiece sharply recurved craniad; sulcus angularis present as constriction within greater curvature immediately proximal to pyloric bend, corresponding constriction in lesser curvature less pronounced; pyloric constriction at sphincter pronounced and symmetrical. Pyloric sphincter asymmetrical, mass of valve considerably larger on greater than on lesser curvature but sphincter not unusually large overall; valve funnel-shaped and directed into duodenum; contributing muscle including circular layer and muscularis mucosae.

Musculature well developed throughout, except in fundic caecum; extensive grouping of fibers into bundles within circular layer; unusual and prominent "notch" in muscle wall of greater curvature; substantial reduction in depth of wall in fundic caecum. Fundic caecum with apex directed

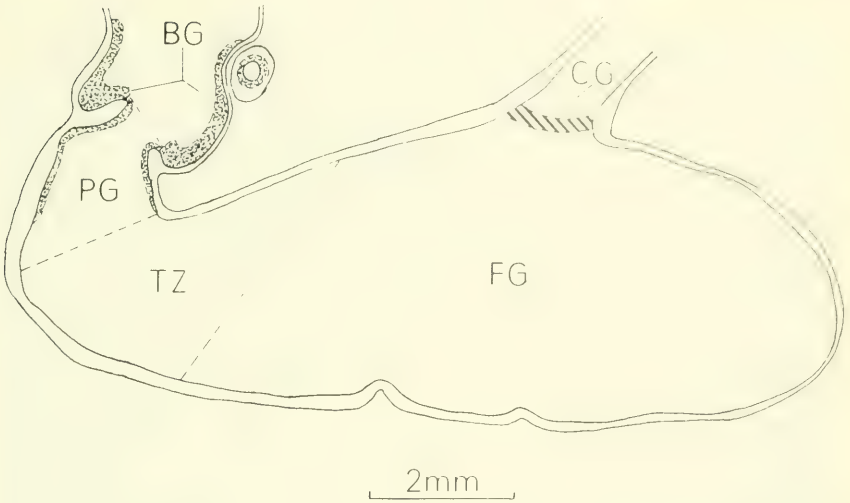


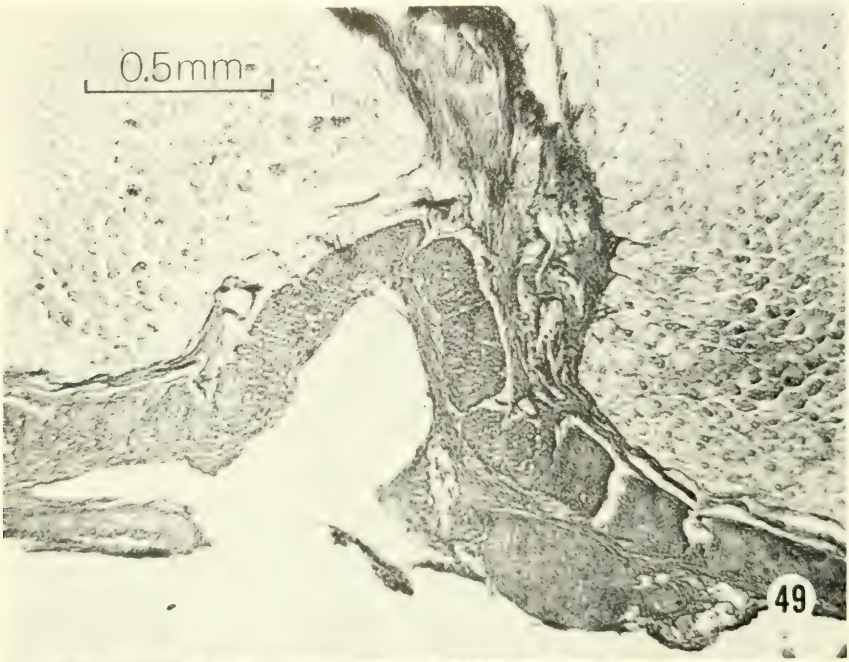
FIG. 48. Mid-longitudinal representation of the stomach of *Molossus ater*. For explanation of symbols, see Figure 3.

slightly postero-laterad in contrast to the antero-laterad orientation in vespertilionids resulting in suggestion of general symmetry to stomach; caecum tapering uniformly laterally, never expanded on dorsal surface; nonmuscular submucosa extremely rare (with exception of prominent loose lamina propria overlying midventral "notch" within greater curvature), elastic fibers extremely sparse in most places and nearly absent within fundic caecum.

Glands of Brunner well developed at, and directly proximal to pyloric sphincter, occurring in single mass at sphincter and as narrow layer within pyloric stomach; terminal end of bile duct dilated at junction with duodenum, resulting in unusual ampule containing duodenal mucosa and submucosal glands of Brunner; stomach in general different in external morphology from those of other carnivorous species examined (see Fig. 48).

Musculature.—Circular layer notably thickened at incisura cardiaca (thickened locally and confined to immediate region of gastroesophageal junction with muscle fibers gathered into long narrow sheets enclosed by septa radiating inwardly from depression at incisura); longitudinal layer not correspondingly thickened at incisura; opposing musculature adjacent to incisura slightly thickened and gathered into bundles locally although anatomical cardiac sphincter probably not present.

Circular layer generally thinner in lesser than in greater curvature; longitudinal layer always extremely thin, except in wall of greater curvature; circular layer irregular in depth, depth moderate at pyloric sphincter on lesser curvature, decreasing sharply at pyloric bend, narrow throughout



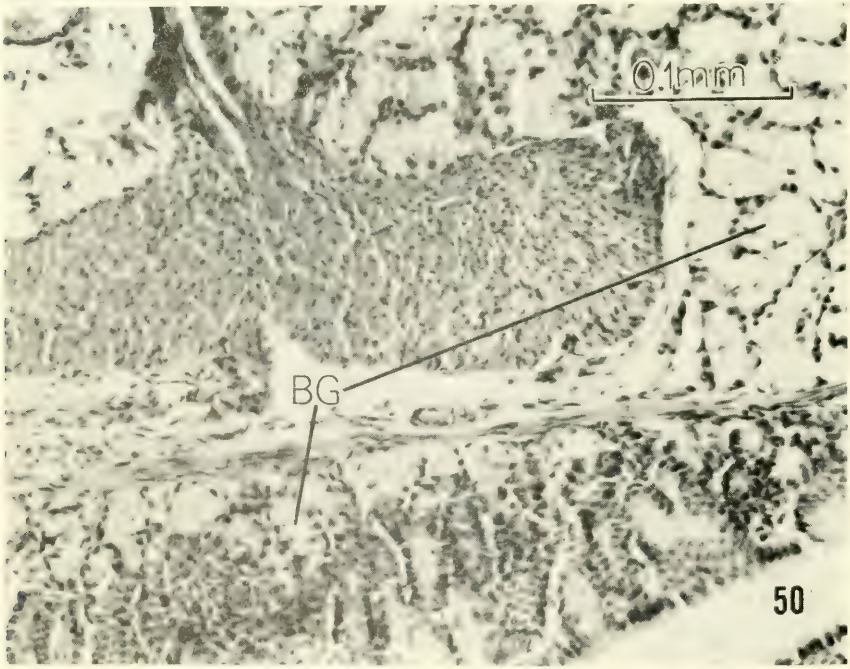


FIG. 49. Midventral cleft in greater curvature of stomach of *Molossus ater*.

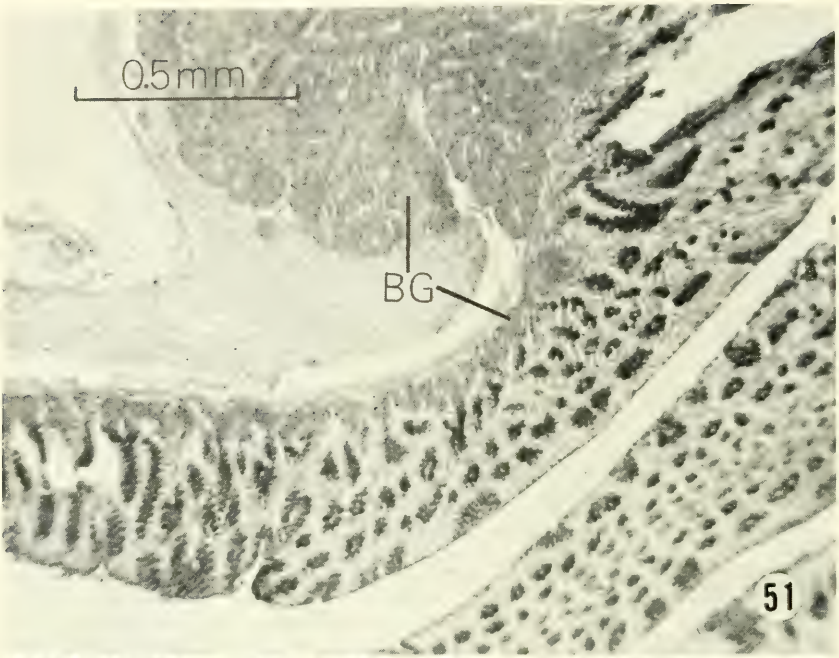
FIG. 50. Pyloric sphincter of *Molossus ater* showing Brunner's gland cells (**BG**) within the stomach.

lesser curvature (excepting cardiac junction) and a thin sheet with some bundling through fundic caecum, increasing to moderate depth through greater curvature to a point proximal to sphincter where layer again narrows; extensive bundling of circular layer occurring throughout most of greater curvature from apex of fundic caecum to midventral "notch." Large, distinctive depression in musculature of stomach wall of greater curvature in frontal half, marked by unusually well-developed submucosa beneath muscularis mucosae and atypically deep fundic mucosa along fold; midventral notch clearly not an artifact as structural disfiguration of muscle layer present (Fig. 49). Musculature generally irregular in depth throughout stomach, especially through fundic caecum and greater curvature, partially owing to extensive gathering of circular fibers into irregularly shaped bundles.

Muscularis mucosae typically double-layered, relatively well developed; uniform in depth throughout stomach. Ganglia of Auerbach's plexus abundant. Depth longitudinal layer 8 to 15, circular layer 15 to 250, muscularis mucosae 15.

Organization of gastric mucosa.—Mucosa consistently gathered into straight, parallel, longitudinal rows throughout most of stomach, with slight zig-zag pattern in walls of fundic caecum lateral to plane of esophageal junction; only major transverse gathering is in greater wall of fundic caecum lateral to midventral notch. Extensive variation in depth of mucosa, generally deeper along lesser than along greater curvature and in tubular stomach (in contrast to caecum); also notable variation in depth within fundic mucosa which is deepest along lesser curvature and along musculature of midventral notch of greater curvature, but is shallow along apex of caecum with extensive variation in depth on both dorsal and ventral walls; marked reduction in number of folds occurring throughout fundic caecum as well; mucosa shallower in furrows than on sides of rugae throughout stomach.

Cardiac glands present and confined to typically narrow zone at gastroesophageal junction; fundic mucosa extensive with marked variation in morphology and depth from one area to another, extending distally to midway between pyloric bend and cardiac junction on lesser curvature, somewhat further on greater arc; extremely narrow transition zone from cardia to fundus; pylo-fundic transition glands (Fig. 48) occupy area between true fundus and pyloric bend, although somewhat deeper into pyloric tube on greater than on lesser curvature; transition zone approximately equal in total length on greater and lesser surfaces; pyloric glands in well-defined region and with unusual basal cell component histologically identical to glands of Brunner; pyloric glands not extending distally beyond proximal surface of pyloric sphincter.



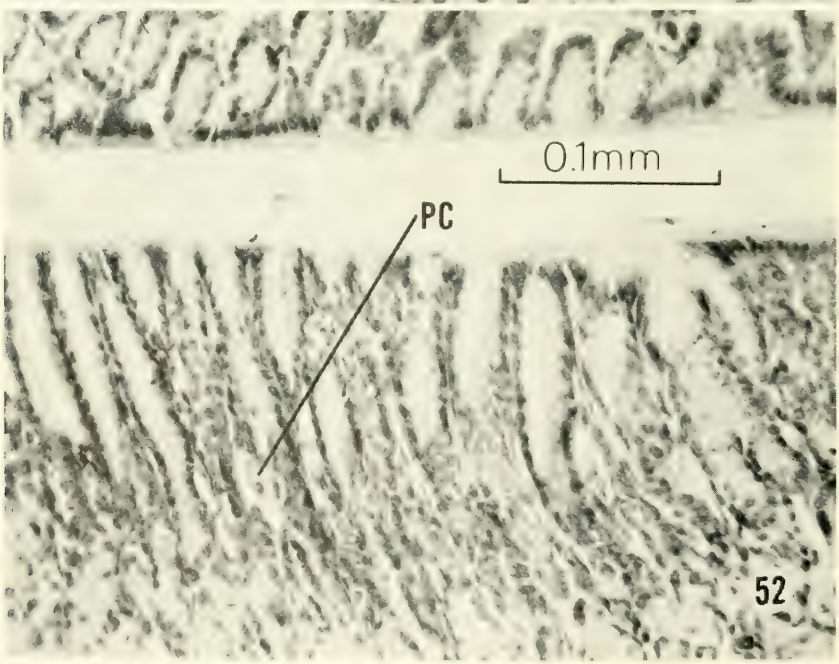


FIG. 51. Glands of Brunner (**BG**) within the duodenum and pylorus of *Molossus ater* (Periodic Acid Schiff Leucofuchsite Reaction).

FIG. 52. Transitional zone of *Molossus ater*. Note the infrequently scattered parietal cells (**PC**).

Glands of Brunner well developed as submucosal glands on distal surface of pyloric sphincter and proximal 2 mm of duodenum (Figs. 50-51), occurring also in pyloric glands as mucosal elements, indistinguishable in morphology from Brunner's glands within duodenum (Fig. 50), also occupying dilated chamber at entrance of bile duct into duodenum; mucosa generally shallow throughout stomach.

Fundic glands deepest in midregion between fundic caecum and transition zone; cardiac glands longer than fundic glands; fundic glands abruptly decreasing in depth in comparison to adjacent cardiac glands; pyloric mucosal membrane slightly deeper than most of fundus, perhaps owing to underlying cells of Brunner's glands, and relatively uniform in depth (deepest at bases of rugae and between adjacent folds).

Cardiac glands.—Glands contained within extremely narrow zone (100 to 200 wide) at gastroesophageal junction; composed of single cell type, cells similar to those of surface epithelium of remaining stomach; glands simple, tubular, of branched type; cells differing from those of fundus in having consistently spherical nuclei throughout; cells small, long and narrow, extremely compact within gland with small, spherical nuclei; glands easily distinguishable from pyloric glands of this species on account of nuclear morphology; glands longer than fundic and pyloric glands and with extremely broad lumen; basal lamina propria scanty; depth of cardiac glands 300 to 360.

Fundus.—Fundic region occupying all of saccular stomach and tubular area up to approximately midway between cardiac junction and pyloric bend. General pattern in distribution of fully developed fundic glands that of a parallelogram with upper facies directed toward fundic caecum; glands with well-developed chief cells extending further into fundic caecum along lesser than along greater curvature (possibly a developmental phenomenon due to flexion of the pyloric tube); glands relatively uniform in cell distribution throughout fundic zone, except glands in apex of fundic caecum which show marked structural reductions; fundic glands usually moderate in length and narrow, extensively convoluted; glands expanded greatly at lower end, less so in upper portion. Most fundic glands uniformly and consistently devisible into three zones, defined by types of cells present; upper third composed of columnar epithelium lining deep gastric pits, middle third composed of parietal cells and mucous neck cells, lower third composed of chief and argentaffin cells; glands of middle and upper fundic caecum marked by substantial increase in length and breadth of gastric pits to 75% length of gland with lower fourth occupied by large infrequent parietal cells mixed with mucous neck cells and occasionally chief cells at base; gradual reduction in number of chief cells at base, gradual reduction in number of chief cells from midregion of stomach to apex of fundic caecum. Depth of fundic mucosa 140 to 260.

Zymogenic cells abundant basally in most of noncaecal fundic mucosa; large, pyramidal with large and spherical nuclei; cells always greater in length than breadth; argentaffin cells commonly observed among chief cells at base and narrowly triangular with extremely large, spherical nuclei, and peripheral argentafile granules.

Parietal cells large and almost always circular with moderately sized spherical nuclei always centrally located; cells usually restricted in distribution to medial third and never abundant; size of cells uniform throughout distribution in given gland with little size increase from bottom to top of zone; found in basal fourth of tubules in fundic caecum but rarely ever observed among zymogenic cells.

Mucous neck cells infrequent beneath base of gastric pit and scattered among parietal cells; nuclei larger than those of parietal cells, cytoplasm minute, cells irregularly shaped. Gastric pits deep; cells lining pits large, with nuclei becoming increasingly more laterally flattened toward surface of mucosa; surface epithelium extremely thick, cells large with extremely large nuclei that are only slightly compressed. Lamina propria always sparse beneath glands but somewhat more extensive beneath muscularis mucosae along greater curvature, owing to buildup of connective tissue around bundles of circular muscle fibers.

Pylo-fundic transition zone (Fig. 52).—Broad zone occupying approximately same area on both curvatures, although distributions not exactly comparable; loss of zymogenic cells gradual within fundus, zone of gastric mucosa lacking chief cells and maintaining parietal cells extending slightly distal to pyloric bend; loss of parietal cells in terminal area also gradual, but more abrupt than termination of chief cells proximally; parietal and mucous neck cells extending to base of glands, although parietal cells less abundant in base than in middle third; gastric pits, surface epithelium, and density of lamina propria equivalent to conditions observed within fundic mucosa; depth 220.

Pyloric glands.—Glands occupy zone within most of stomach between pyloric bend and pyloric sphincter; deepening of gastric pits gradual through terminal portion of transition zone with parietal cells disappearing gradually; basic pyloric gland morphology similar to that observed in other bats, but unusual in presence of apparent layer of glands of Brunner beneath entire distribution of pyloric mucosa and hence contributing to the depth of the mucosal membrane (see section on glands of Brunner); mucous cells of pyloric glands large; nuclei extremely large, becoming progressively more flattened laterally from bottom to top of gland; pyloric glands increasing in breadth from base of gland as cells increase in size, lumen also becoming progressively broader upwards; depth of pyloric glands irregular but generally deeper on lesser than on greater curvature; surface epithelium

extremely thick, slightly thicker than that of fundus; depth of pyloric glands 120 to 200.

Glands of Brunner.—Glands well represented as a single mass in submucosal distribution along distal surface of pyloric sphincter and proximal 2 mm of duodenum; also found in terminal dilation of bile duct (also submucosal) and directly beneath entire complement of pyloric mucosa (usually above muscularis mucosae) as thin layer of glands reduced in size; duodenal glands long and narrow, highly convoluted with small, pyramidal cells; nuclei large, peripheral, ovoid to substantially flattened laterally; cytoplasm pale pink and diffusely granulated when stained with Harris' haemotoxylin and eosin; glands always submucosal; those within mucosa of pylorus approximately half diameter of duodenal complement (Fig. 51), highly convoluted, both mucosal and submucosal (observed between two layers of muscularis mucosae) although usually within mucosa; occurring also at base of mucosal membrane between adjacent pyloric glands; cellular morphology of pyloric complement identical to that in duodenum, lumen narrow in both.

Remarks.—The tube-like stomach of *Molossus* presents a perplexing array of features; most features represent conditions observed in other insect-feeding bats. The stomach, however, although tubular, is less symmetrical in outline than is that of other carnivorous bats and has the elongate terminal stomach usually observed in bats that are primarily or entirely herbivorous. The pyloric sphincter is moderately developed, asymmetrical, as in *Plecotus*.

The gastric mucosa is uniformly gathered longitudinally through the simple, unpartitioned fundic caecum. The patterns of distribution of cellular elements within the fundic mucosa and variations within the fundic caecum are essentially as observed in *Plecotus*. The most noteworthy feature of the gastric mucosa is an extremely thin layer of narrow, convoluted, tubular glands which are histologically indistinguishable from the glands of Brunner in this species and which lie immediately beneath the zone of pyloric mucosa. These serous tubular elements are less conspicuous and presumably less abundant than the corresponding layer of glands observed in *Sturnira*. In one specimen of *Molossus*, the sub-pyloric glands appeared to be in discontinuous masses near the proximal surface of the pyloric sphincter, suggesting less complete invasion into the stomach than observed in specimens of *Sturnira*.

One unusual feature observed only in *Molossus* is a deep and prominent transverse cleft in the stomach wall that is located along the greater curvature. This depression is clearly not an artifact of fixation or preparation, or a contractional wave within the stomach musculature, because the cleft is accompanied internally by a distinctive break in the muscle layers, a

heavy local concentration of lamina propria, and slightly deeper gastric mucosa than in adjacent areas. It is further of interest that Rouk (1968), in his description of the stomach of a molossid, *Tadarida brasiliensis,* described and illustrated a single depression midway along the greater curvature that appears to be identical to that described here for *Molossus.*

Rouk's description of the stomach of *T. brasiliensis* suggests further noteworthy similarities between that species and *Molossus ater.* The general stomach outline is similar, although curvature of the stomach anteriorly is greater in *T. brasiliensis.* The fundic caecum in both species tapers to a narrow apex, and the orientation and position of the gastroesophageal junction and structure of the pyloric sphincter appear to be identical in the two. Neither species has a cardiac vestibule, and both have an elongate, cranially reflected, terminal pyloric endpiece.

HISTOCHEMISTRY OF THE GASTRIC MUCOSA AND DUODENAL JUNCTION

The results that follow are limited to a survey of basic types of reactions for mucosubstances, and are to be regarded as necessarily preliminary to more detailed studies. To my knowledge, the present study (excepting the brief PAS-Alcian blue account of surface epithelial mucus of Rouk, 1968) is the first discussion of comparative mucopolysaccharide histochemistry of the gastric mucosa of bats. The following accounts are directed to the identification and discussion of neutral and acid mucopolysaccharides as demonstrated by toluidine blue O metachromasia, PAS, and Alcian blue 8GX 300. No attempt was made to identify specific chemical end-groups, because the objective of the study was to examine and characterize mucin specificity in species of bats relative to each other. More detailed discussion of specific categories of mucin are to be found in the accounts of techniques to follow, where a particular technique was most appropriate in mucin identification.

Periodic Acid Schiff Reaction

The PAS reaction is generally thought to indicate the presence of neutral mucopolysaccharides, and, because most mucins are apparently colored with this procedure, it also provides a general indication of overall mucous activity. Mucins stain red or magenta with this procedure.

In any test for the presence of complex carbohydrate material, it is necessary to account for the potential reactivity of lipids and simpler carbohydrates. As a check for the presence of distinctive concentrations of glycogen, sections of stomachs of each species were subjected to digestion by salivary amylase for 10 minutes at room temperature, prior to oxidation by periodic acid. In no case was glycogen, or other material presumably

removed by exposure to amylase, found to be a contributing factor to the intensity of PAS reactivity in sites of production of mucin material.

Using PAS, staining cells of the glands of Brunner always was uniform throughout the cytoplasm, with no apparent local areas of especially high intensity. Staining of surface epithelium was restricted to a narrow border of mucous droplets along the luminal surface (surface opposite to base), except for slight additional staining of fine cytoplasmic granules just beneath the luminal mucous material in one species (*Plecotus*). Parietal cells stained uniformly throughout the cytoplasm, but mucous neck cells stained only within the cytoplasmic material between the nucleus and lumen of the tubule (outer portion of cytoplasm). All cells within the cardiac and pyloric glands, irrespective of location, stained only with the luminal portion of the cytoplasm. The above statements apply equally well to those cells that stained with Alcian blue, except for an apparently more complete staining of the mucous neck cell cytoplasm with Alcian blue in the case of *Phyllostomus.*

A uniformly strong reaction characterizes the surface epithelial mucus of all species of bats with the exception of *Desmodus,* in which the reaction is only slightly reduced in intensity in comparison to the other species examined. An equivalent statement may be made concerning the gastric foveolae of the fundic, pyloric, and cardiac glands of *Desmodus,* excluding the lower portions of cardiac and pyloric tubules to be discussed later. Staining was noticeably stronger in the foveolae within the fundic caecum in contrast to the remainder of the fundus in two species, *Glossophaga* and *Carollia.* Duodenal goblet cells of all species examined reacted with a uniformly high degree of intensity.

The glands of Brunner reacted relatively weakly in *Rhynchonycteris, Plecotus* and *Pizonyx,* moderately in *Artibeus* and *Sturnira,* and strongly to extremely strongly in the remaining species. Identical qualities of reactivity in the glands of Brunner of the duodenum and the basal cell complexes within the pyloric stomachs of *Sturnira* (Fig. 28) and *Molossus* (Fig. 51) help to confirm their previous identification, on morphological grounds, as glands of Brunner. Genera of the family Phyllostomatidae (excluding *Sturnira* and *Artibeus*) and the single noctilionid consistently revealed the greatest degree of reactivity in the glands of Brunner.

Deeper cellular elements of the fundic mucosa revealed highly varied reactivity to PAS. Mucous neck cells among parietal cells react consistently less than surface or foveolar epithelial cells, except for equivalent reactivity in the case of *Noctilio.* The frugivores (*Carollia, Sturnira,* and *Artibeus*), as a group, showed less reactivity within the mucous neck cells in comparison to carnivorous species, except for extremely weak coloring in *Desmodus* and virtually no positive coloring at all in *Plecotus* and *Myotis.*

Little mention has been made in the literature of PAS reactivity, positive or negative, of gastric parietal cells. Leblond (1950) noted that the parietal cells of albino rats stain "weakly" with a periodic acid-fuchsin-sulphurous acid procedure, approximately equivalent to PAS, and suggested that some mucin activity might be attributable to parietal cells. A clearly positive staining in parietal cells, over and above that of several other gastric elements that are clearly PAS positive, was observed in several species of bats. Only a trace of reaction was observed in carnivorous bats, except for a weak reaction in the blood-feeding *Desmodus,* and moderate staining in *Molossus.* The presumably partially nectivorous and partially carnivorous *Glossophaga* revealed moderately stained parietal cells, as did three frugivorous species.

Although Lillie (1965) recorded positive PAS reactivity in the zymogenic granules within the salivary glands of man and several species of rodents, and in the pancreatic zymogen granules of man, rabbits, and some mice (but not in rats or guinea pigs), little or no information appears to be available regarding such reactivity in the zymogenic granules of gastric chief cells. Little or no staining was observed in gastric zymogenic cells of the bats examined, with the exception of a consistently strong (+4) staining of the zymogenic granules in two specimens of *Noctilio.* The significance of this result is unknown.

As noted previously, the major portions of the cardiac and pyloric foveolae stain intensely with PAS, with little variability among species. In contrast, the lower one-third to one-tenth, depending upon the species, of the cardiac and pyloric tubules were found to always stain less intensely than the remainder of the tubule (excepting the equivalent reaction in the pyloric glands of *Molossus*). A reasonable explanation for this might be that less total mucous material is present in the basal portions of the tubules than within the upper border. However, little physiological evidence is available to confirm such a statement, and results of staining with Alcian blue, discussed beyond, tend to refute this idea as well. Loss of staining capacity within the basal portion is abrupt from one cell to the next, suggesting a specific loss of some cellular material within the basal area. The degree to which the basal area stains in contrast to the remainder of the tubule depends upon the glandular area under consideration, and the species examined.

In the case of the cardiac glands, basal reactivity is only slightly less (+3 or +4) than in the remainder of the gastric tubule (+5), except for marked decreases (+1 or trace) in the cases of *Plecotus* and *Pizonyx.* A similar pattern was observed in the pyloric glands, but several additional species, all carnivorous, revealed marked reduction in basal reactivity. Basal portions of the pyloric glands of *Plecotus* and *Pizonyx* revealed little or no reactivity. Also, the pyloric glands of *Rhynchonycteris* and *Molossus* had

little reactivity in the basal area. All the phyllostomatids and *Natalus* revealed only slightly less basal staining in the pyloric glands in comparison with the remainder of the tubule.

Overall production of neutral mucins, as revealed by PAS, appears to be relatively uniform among bats examined. There is clearly generalized reduction in intensity of PAS reactivity throughout the stomach and upper duodenum of *Desmodus,* although relatively slight in comparison to other bats. Species exhibiting especially high levels of secretion of gastric mucins demonstrated by PAS include *Noctilio, Pizonyx, Molossus,* and particularly by *Phyllostomus.*

Because results of PAS are uniform among species for a number of glandular and cellular elements, it is difficult to draw conclusions regarding relationships between and among the bats studied. It is of interest to note, however, that certain pairs or groups of bats are nearly identical, yet unique, in reactivity in the spectrum and combinations of glandular or cellular types showing particular degrees of staining capacity. *Plecotus* and *Pizonyx* are nearly identical in reactivity, differing slightly only in the basal portions of the cardiac glands. *Sturnira* and *Artibeus* are equally similar, as are *Pteronotus* and *Phyllostomus.* Members of the Phyllostomatidae are not equivalent in reactivity of all gastric regions examined. Carnivorous and partially carnivorous phyllostomatids can be separated from frugivorous kinds by the intensive staining in the lower mucous neck cells and weaker staining in the parietal cells. *Glossophaga,* principally a nectivore that also eats some insects and fruit, evidences staining of the lower mucous neck cells and nearly equally intensive staining of parietal cells. The most unusual bats in terms of patterns of staining are *Noctilio* with heavily stained zymogenic granules, and *Desmodus,* which exhibits overall reduction in presence of PAS positive mucus.

Reaction to Toluidine Blue O

Toluidine blue O stains mucous material either orthochromatically (blue) or metachromatically (reddish-purple). Toluidine blue metachromasia is thought to indicate the occurrence of sulfated acid mucopolysaccharides.

To test for the presence of hyaluronic acid which may stain metachromatically, tissue sections were exposed to an aqueous medium of testicular hyaluronidase, which presumably digests both hyaluronic acid and several chrondroitin sulfates. No demonstrable alteration of local metachromasia was observed in any species after 18 hours digestion at 40° C. These results suggest absence of hyaluronic acid and chrondroitin sulfates, at least as distinctive components of certain metachromatically staining regions under study.

A summary of the results of toluidine blue staining is shown in Table 1.

TABLE 1. Toluidine blue metachromasia.

Species	Area of Reactivity					
	Gastric foveolae	Glands of Brunner	Pyloric glands	Cardiac glands	Mucous neck cells	Goblet cells
Rhynchonycteris naso	+ (tr)	−	−	−	−	+
Noctilio labialis	−	+ (tr)	−	+	−	+
Pteronotus parnellii	−	+ (tr)	−	+	−	+
Phyllostomus discolor	+	+ (tr)	−	+	−	+
Glossophaga soricina	+	+ (tr)	−	+	−	+
Carollia perspicillata	−	+	−	−	−	+
Sturnira lilium	−	−	−	−	−	+
Artibeus lituratus	−	−	−	−	−	+
Desmodus rotundus	−	−	−	−	−	+
Natalus stramineus	−	+ (tr)	−	+ (tr)	−	+
Plecotus townsendii	+ (tr)	+	+	+	−	+
Pizonyx vivesi	+	−	+	+	−	+
Molossus ater	−	+	−	+ (tr)	−	+
Control (*Peromyscus*)	−	+	−	+	−	+

Some slight variation in staining was noted in the glands of Brunner between individual specimens of two species (*Plecotus townsendii* and *Carollia perspicillata*), but the reaction to this stain of specimens of all other species was uniform for a given gland. This observation complements the negative results of sulfate autoradiography of Jennings and Florey (1956) in surface epithelia of several species of rodents. Decidedly positive reactions were widespread in the foveolae of fundic glands only in *Rhynchonycteris* and *Phyllostomus*, and in the fundic caeca of *Plecotus* and *Pizonyx*, with slight reactivity in the fundic caecum of *Glossophaga*. Sections of the stomachs of two rodents used as controls (*Peromyscus leucopus* and laboratory-raised *Mus musculus*) yielded no metachromatic staining in either surface epithelia or gastric foveolae.

The most consistently positive metachromatic staining was observed in the goblet cells of the upper duodenum. All species examined yielded a distinctly positive metachromasia.

Well-defined patterns of positive metachromasia within systematically related groups or among bats with similar food preferences were not observed. It is of interest to note, however, that only *Phyllostomus* yielded a positive metachromasia in the deeper mucous neck cells. Also, the two specimens of *P. discolor* examined demonstrated the greatest overall metachromasia within the seven regions of the stomach considered, apparently indicating atypically well-developed sulfate mucous material(s) in that species. The results also suggest that noncarnivorous species, especially

frugivores like *Sturnira* and *Artibeus,* contain comparatively less metachromatic material, and hence mucous material with sulfate groups, than do most carnivorous species. There are exceptions, however, and additional studies involving more species and numbers of species are required to test this point. *Desmodus* shows definite overall lack of gastric metachromasia, although perhaps for different reasons than the frugivores. Little is known regarding the physiological role of gastric mucins in general, and less with specific regard to those with sulfate ester linkages (if indeed toluidine blue metachromasia demonstrates such substances).

All stomachs examined were devoid of gastric contents and, therefore, supposedly were in relatively equivalent physiological states with respect to mucus production; the variability observed in response of mucins to toluidine blue O probably reflects true differences among the species studied.

Reaction to Alcian Blue

The Alcian group of dyes, including Alcian blue, green, and yellow are thought to denote the occurrence of acid mucopolysaccharides by way of coloration of carboxyl groups. Mowry (1963) noted that Alcian blue closely approximated the results of Hale's reaction (Hale, 1946) for acid polysaccharides.

The Hale colloidal iron procedure was tried twice on sections of stomachs of bats, but results were entirely negative for every species, perhaps a result of inappropriate fixation.

Two different, although similar, Alcian blue tests were conducted. In the bats studied, reactions to the two procedures utilizing Alcian blue were generally comparable excepting where cardiac and pyloric glands were involved.

Exposure to periodic acid prior to staining with Alcian blue was reported by Mowry (1963) to demonstrate the presence of glycogen. No distinctive concentrations of glycogen were found in my study by the use of this procedure.

Goblet cells of the upper duodenum reacted strongly to both Alcian blue procedures in every species examined. Spicer (1960) noted that acid differentiation appeared to increase staining of sulfated mucins by Alcian blue; however, in light of the clearly positive reactivity in the absence of periodic acid oxidation, it appears safe to suggest that both sulfated and non-sulfated mucosubstances occur in the goblet cells of most, if not all, bats examined. These results are entirely consistent with those obtained by Spicer (1960) for three species of rodents and a rabbit.

The duodenal glands of Brunner revealed strongly positive reactivity with Alcian blue in only one species, *Carollia,* in contrast to considerably more widespread toluidine blue metachromasia in these glands among the species of bats (see Table 1). Staining of mucins within the glands of

Brunner not only occurred in two specimens of *Carollia* but was exceedingly strong. Although positive reactivity might have been the result of sulfated mucosubstances known to be present by the results of toluidine blue tests, this prospect seems unlikely in the absence of positive results in any other species. A trace of Alcian blue staining was observed in Brunner's gland cells of *Sturnira* and *Artibeus*, but it is difficult to justify this as resulting from the presence of mucosubstances because there was no contrast with the surrounding tissue. The basal-most cell complex within the pyloric stomach of *Sturnira* revealed but a trace of staining, and that of *Molossus* revealed none, perhaps further justifying the identification of glands of Brunner within the stomachs of these two bats.

A weak to strong reaction was recorded in the gastric surface epithelium of the cardiac stomach of all species examined excepting *Sturnira*, *Artibeus*, and *Desmodus*. The epithelium of *Sturnira* and *Artibeus* stained only with a trace, that of *Desmodus* not at all. Results were nearly identical between the two Alcian blue procedures, with no distinctive differences requiring evaluation.

Surface epithelial cells of the fundus reacted positively to Alcian blue, although consistently slightly less than the cardiac epithelium in most species. *Rhynchonycteris* and *Phyllostomus* would seem to be exceptions to this trend by showing equality of reactivity in the two glandular regions, and *Desmodus* revealed moderate staining in the fundic epithelium in contrast to none at the surface of the cardia. Several species demonstrated decreasing reactivity of the surface epithelium with Alcian blue through the terminal portion of the fundus and through the pyloric zone to the pyloric sphincter. These included all carnivorous species and *Glossophaga*, but not the three frugivorous species or the sangivorous *Desmodus*. This reduction in staining quality probably represents a progressive decrease in reactive material from the midstomach toward the pyloric sphincter. This condition is especially interesting in light of the often observed increase in depth of the surface epithelium from the fundic mucosa through the pylorus.

Reactions of cells within the cardiac glands are highly variable between portions of a single tubule, among species, and between the two procedures for certain species. As in the case of PAS, the upper neck as well as various relative percentages of the basal portion of tubules stain differentially with Alcian blue. Whereas reaction to Maxwell's Alcian blue tends, in most species, to correspond with results observed with PAS (that is, staining within the basal portion is less than that observed in the neck region), a simple exposure to aqueous Alcian blue (Steedman's procedure) revealed the reverse situation in *Natalus*, *Plecotus*, *Pizonyx*, and *Molossus*. In these genera the basal area stained more intensely than the neck. The cardiac glands of *Sturnira* yielded no positive staining with either procedure; those

of *Artibeus* stained weakly and equally throughout the tubule with both procedures. The aqueous reaction (Steedman's) for the remaining seven species was moderate to strong, and either equal in strength throughout the tubule, or less in intensity in the basal area (seen also in these seven species using Maxwell's procedure). The pattern of overall relative response to Alcian blue between cardiac glands of different species was roughly equal between the two procedures, although Steedman's was consistently slightly more intensive than Maxwell's.

In summary, the results of staining cardiac glands with Steedman's Alcian blue revealed a pattern of distribution into one of three categories, depending upon the presence or absence of reversed differential staining within the tubular glands of the cardia. One group that had differential staining with the aqueous Alcian blue procedure reversed to that of PAS is composed of *Natalus, Plecotus, Pizonyx,* and *Molossus.* A second group, composed only of *Sturnira* and *Artibeus,* showed little or no reactivity throughout the cardiac tubules. The last group included all remaining species in which the cardiac glands reacted moderately to strongly, either in a pattern similar to that of PAS (basal staining less than upper portion) or with uniform staining throughout the length of the tubule.

Results for Alcian blue staining of pyloric glands were somewhat similar to those obtained in the cardiac mucosa. Reversed (to that of PAS) differential staining occurred after exposure to Steedman's Alcian blue procedure in three (*Natalus, Plecotus, Pizonyx*) of the four species in which this was demonstrated for the cardiac glands (and with increased intensity relative to Maxwell's procedure, also seen in the cardiac glands). The basal portions of the pyloric glands of these three species stained moderately to intensely, whereas the necks gave only a weak reaction (*Molossus* revealed only slight staining throughout the pyloric glands). Using Maxwell's procedure, basal portions of the pyloric glands of these species were consistently unstained and reactions in the necks were weak to moderate. *Sturnira* revealed no staining of pyloric glands with either procedure; *Artibeus* stained slightly in the neck region, but only when Maxwell's procedure was used.

None of the remaining species showed reversed differential staining in the pyloric glands. Except for *Glossophaga* and *Carollia,* the pyloric glands of which reacted uniformly and strongly only to Steedman's procedure (and with complete lack of staining after periodic acid oxidation), there is a clear trend within remaining genera studied toward more intense staining of mucus using Maxwell's procedure. *Rhynchonycteris, Pteronotus, Phyllostomus,* and *Desmodus* reacted only with Maxwell's procedure. None of the species of the Emballonuridae, Noctilionidae or Phyllostomidae demonstrated the reverse differential staining discussed previously.

In summary, it may be said that the cardiac and pyloric glands in

considerably more similar histochemically among species in the Natalidae, Vespertilionidae and Molossidae, than among the Emballonuridae, Noctilionidae, Desmodontidae and Phyllostomatidae, with the exception of the uniformly poor reactivity of the phyllostomatids *Sturnira* and *Artibeus*. The results included here would seem to refute contentions by some workers that pyloric glands and glands of Brunner may be equivalent gastrointestinal entities.

The mucous neck cells of the fundic mucosa of *Rhynchonycteris, Noctilio,* and species of the Phyllostomatidae (excluding *Phyllostomus, Sturnira* and *Artibeus*) stained weakly to intensely with Steedman's procedure, but stained only slightly or not at all with Maxwell's. *Phyllostomus* stained strongly with both procedures, whereas *Sturnira* revealed no staining in the mucous neck cells and *Artibeus* showed only a trace of staining with Steedman's method. The mucous neck cells of *Desmodus* did not react to Alcian blue. The remaining four species of the Natalidae, Vespertilionidae, and Molossidae revealed an interesting pattern of coloration. The mucous neck cells of *Natalus* reacted moderately to Maxwell's procedure, but did not stain with a simple aqueous method. In contrast, those of *Plecotus, Pizonyx* and *Molossus* all stained moderately with the aqueous procedure; the first and last species showed a trace of staining with Maxwell's procedure but *Pizonyx* did not.

In comparing the results obtained with PAS and Alcian blue, the most notable immediate contrast is that observed in the glands of Brunner. Although Lillie (1965) recorded these glands as staining only red in a combined PAS-Alcian blue procedure, suggesting negative results in terms of Alcian blue, Spicer (1960) reported that although these glands in mice and rats react as indicated by Lillie, Brunner's glands of guinea pigs and rabbits yielded a moderate to strong reaction to an aqueous solution of Alcian blue. *Carollia* appears to represent an example of the latter condition among bats.

It is apparent that variation exists among species of bats in the presence or absence and degree of reactivity to Alcian blue in various mucous cells, hence in relative amounts of acid mucosubstances, and is substantially greater than the reactivity of relatively neutral materials stained with Schiff's reagent. The fact Alcian blue at pH 7.1 may show greater specificity in reactivity with various substances than does Schiff's reagent may be a contributing factor to this variability.

Summary.—In summary, acid and neutral mucopolysaccharides of epithelial, gastric and Brunner's gland secretions react variably to a greater or lesser degree to four histochemical procedures that demonstrate the presence of mucin materials. Variability in reactivity of gastric and duodenal mucins to toluidine blue is extreme among carnivorous species;

herbivores and a single sanguivore are uniformly unreactive in all but goblet cells mucins. The results of PAS and Alcian blue procedures reveal interesting patterns of staining in certain portions of the gastric mucosa that suggest unique combinations of various mucin materials within closely related families or subfamilies of bats, and reveal evidence that bats with markedly different food preferences have different qualitative and quantitative mucopolysaccharide complements.

Mucin Histochemistry of the Stomach in Relation to Food Habits

The utilization of four histochemical procedures, thought to be specific for complex mucopolysaccharide substances, has revealed interesting trends and similar patterns of reactivity among certain phylogenetically and nutritionally related groups of bats.

The most extensive gastric mucous production of any bat examined was that of *Phyllostomus discolor*. Mucins of this species reacted consistently and with high intensity to all three procedures employed, and these results reflect the presence of a particularly well-developed gastric mucosa in this bat. The omnivorous diet and seemingly ravenous feeding habits of this species evidently require abundant surface mucus to replenish a rapid loss of large quantities in escaping chyme. The omnivorous habits of *Phyllostomus* probably are related to comparatively extensive secretion of metachromatically staining gastric mucus and to equally extensive neutral epithelial mucins. In addition to the extensive mucous material in the stomach of *Phyllostomus*, as revealed by tests with PAS, the strongly positive results from both Alcian blue procedures indicate that chemical diversity of acid mucins may be more extensive in this bat than in most other species.

Histochemical results indicate that the three frugivorous species and the sangivorous *Desmodus* are comparatively low in production of gastric mucins, including surface as well as deeper mucous cells. It is clear, however, that *Carollia* far exceeds *Sturnira* and *Artibeus* in production of gastric mucus, and approaches the moderate condition of *Glossophaga*. Moderate reactions to PAS were recorded for the surface epithelium of *Artibeus* and *Sturnira*, although the quantity of mucus present was low for each. Toluidine blue and Alcian blue reacted weakly in these two species.

In all bats but the frugivores, the surface epithelial mucin demonstrated by Alcian blue was found to decrease progressively in reactivity through the terminal portion to the pyloric sphincter; this epithelium stained consistently to the sphincter in the obligate fruit-eaters. This suggests the possibility of more widespread secretion of mucin in the stomachs of the latter group.

In overall mucous production, the primarily nectivorous *Glossophaga* tends to resemble insectivorous and carnivorous species more than frugi-

vores, although it is notably similar to *Carollia* in several features. Mucous material, as revealed by PAS and Alcian blue, is more abundant throughout the stomach of *Glossophaga* than the three frugivorous kinds, although less abundant than in *Pteronotus* or *Phyllostomus*. *Glossophaga* also reveals greater diversity of cell types yielding a demonstrable metachromasia than do any of the frugivorous species (diversity also is the tendency in insectivorous species in this regard). *Glossophaga* and *Carollia* are similar and unique, however, in the greater intensity of staining of the gastric foveolae within the fundic caecum in contrast to the remainder of the fundic mucosa (absent in other species, even in those with deepened gastric pits in the fundic caecum). Additionally, *Glossophaga* shows intensive staining of the lower mucous neck cells, otherwise restricted to insectivorous and carnivorous species, and this, in combination with the moderate reactivity of parietal cells to PAS noted above, clearly suggests the presence of an intermediate condition relevant in mucin production in this species. It is of interest to note that the parietal cells of the three frugivorous species (also *Glossophaga*) react moderately strongly with PAS, but there is no comparable result in any purely insectivorous or carnivorous species. The possibility exists, although admittedly remote, that the parietal cells of these frugivores may assume a mucus-producing function in the absence of the surface epithelial mucus found to occur in most other species of bats, in addition to their function as the probable source of hydrochloric acid.

It has been fairly well established that mucous production is slight in the stomach of *Desmodus,* in surface and deeper mucous material, as well as in secretions from the glands of Brunner. In the absence of numerous parietal and chief cells, there is little probable need for surface mucus as a protective device against autodigestion, and the non-abrasive nature of the primary food source of this species would suggest little need for epithelial mucus as a lubricant against mechanical injury.

Most insectivorous and carnivorous species of bats yielded moderate to strong reactions (PAS) for neutral epithelial mucins, and for acid mucopolysaccharides as demonstrated by Alcian blue. As regards overall mucous production, relatively little information emerges, using the general techniques employed in this study, to suggest differences between insectivorous and piscivorous species. However, the mucins of the cardiac and pyloric glands of *Pizonyx* revealed particularly strong metachromasia with toluidine blue, and the epithelial mucins in these two glandular areas may be generally thought of as uncommonly abundant. In comparison to its relative, *Plecotus,* and from what can be gathered from the work of Rouk (1968) on two other vespertilionid bats, the cardiac and pyloric glands of *Pizonyx* are morphologically and physiologically distinctive elements in this bat, and for reasons that are unclear provide particularly abundant mucus at the two gastric orifices.

Some considerable variation exists in reactivity of the deeper cells of the cardiac and pyloric glands to particular procedures among insectivorous species, particularly for the two Alcian blue techniques. Because this variation appears to have greater systematic than morphologic application, a discussion of it is deferred to a later section. Insectivorous, piscivorous, and nectivorous species reveal heavier complements of gastric mucus in the neck cells of the cardiac and pyloric glands than do obligate fruit-eaters and the sangivorous *Desmodus*.

The unique presence, among the bats studied, of PAS-reactive zymogenic granules in the stomach of *Noctilio* is not readily explainable.

Toluidine blue metachromasia is considered by most, including Spicer (1960, 1963), to demonstrate the presence of sulfated acid mucopolysaccharides. This belief is supported by autoradiographic analyses of ^{35}S absorption in the gastric mucosa of several species of rodents and one rabbit as presented by Jennings and Florey, 1956; these show general conformity in $^{35}SO_4^{=}$ uptake in areas correspondingly demonstrating toluidine blue metachromasia. Metachromasia may occur in some neutral mucopolysaccharides such as those of the glands of Brunner but Wislocki *et al.* (1947) suggested that hyaluronic acid may account for some metachromasia in tissue sections. Tests for hyaluronic acid were negative in all species examined suggesting a lack of this substance in the gastric mucus of bats.

Reactivity to toluidine blue O in the form of observable metachromatic staining reveals extensive variability between species and families, and among carnivorous species generally. Non-carnivorous species within the Phyllostomatidae tend to show less reactivity than do the carnivorous members examined. A principally nectivorous phyllostomatid, *Glossophaga*, which apparently often takes insects in the diet, had greater diversity of areas showing positive reactivity (as in the strictly carnivorous types) than did the three frugivorous phyllostomatids. The two species examined of the Vespertilionidae were notably similar, although not identical, in pattern of metachromatic staining.

The glands of Brunner, although not an element of the stomach in most species, are morphologically and physiologically closely associated with the stomach, and therefore were examined histochemically. The glands of Brunner of all species revealed some PAS-positive material, whereas toluidine blue gave mixed results, and only *Carollia* yielded a positive staining with Alcian blue. It would appear that the glands of Brunner of *Carollia*, although extremely limited in distribution, are unusually active in the secretion of an abundance of neutral, as well as acid mucopolysaccharides.

Species variability in reactivity of Brunner's glands to PAS has been shown to exist in rodents by Spicer (1960). He noted that Brunner's

glands of albino mice stained weakly, those of rats stained moderately, and those of guinea pigs stained more intensely than either rats or mice. The physiological significance of such variability is unknown. It is of interest to note that Lillie (1965:511) recorded the glands of Brunner as negative to Alcian blue, and it would appear that *Carollia* and perhaps *Sturnira* and *Artibeus* may represent genera within subfamilies of bats unusually adapted for mucous production by the glands of Brunner. Relatively neutral mucin material appears to be most consistently represented in the Brunner's glands of the insectivorous or partially insectivorous Phyllostomatidae, Noctilionidae, and Molossidae. The results of PAS, as noted previously, confirm the presence of Brunner's glands in the stomachs of *Sturnira* and *Molossus*.

GASTRIC MORPHOLOGY IN RELATION TO FEEDING

Food Habits of Species Examined

Relatively little as yet is known concerning the specific nature and geographic variability of food habits for most species of bats. Therefore, we can only generalize regarding feeding preferences of certain species.

Little or no information appears available regarding the specifics of food habits of *Rhynchonycteris naso* or, indeed, emballonurid bats in general. Goodwin and Greenhall (1961) noted that *R. naso* on Trinidad and Tobago, along with all other species of sac-winged bats on these islands, feed exclusively on insects. Perhaps mostly small, soft-bodied prey species are taken by this bat and are macerated to the point that identification is difficult.

Noctilio labialis, unlike the fish-eating *N. leporinus,* appears to be an obligate insect-feeder as noted by Bloedel (1955) and Hooper and Brown (1968). According to Hooper and Brown, beetles, Lepidoptera, and bugs comprise a large portion of the diet of *N. labialis.* Numerous species of the Phyllostomatidae, long thought to be almost completely herbivorous or nectivorous, are now known to be in part insectivorous or carnivorous as a result of recent food habit analyses. A number of kinds including *Pteronotus parnellii* are as yet poorly studied. *P. parnellii* has been reported to be an obligate insect-feeder. *Phyllostomus discolor* was reported by Goodwin and Greenhall (1961) to eat only fruit, but Arata *et al.* (1967) observed insect remains in the stomach of *P. discolor,* noting that the genus *Phyllostomus* is omnivorous. The omnivorous habits of a closely related species, *P. hastatus,* are well documented (Dunn, 1933; Arata *et al.,* 1967). *Glossophaga soricina* is a nectar-feeder, but feeds additionally on soft fruits (Arata *et al., op. cit.*) and is known also to take large insects, thus discounting the hypothesis that some insects are taken only incidently with ingested fruit. Although *Carollia perspicillata* is primarily a consumer of soft, pulpy fruit, Arata *et al.* (1967) noted that the stomach contents of

more than a fifth of the specimens of this species examined by them contained quantities of insect material. Also noted was a single instance of either cannibalism or predation on another bat. It would appear, on the basis of present information, that *C. perspicillata* is not truly an obligate fruit-eater, although it probably is less an omnivore than *Glossophaga* or *Phyllostomus*. *Sturnira lilium* is clearly an obligate fruit-eater. *Artibeus lituratus* may occasionally take some insects in the diet, although it consumes mostly soft fruits, apparently in great quantities, as food material passes through the digestive tract quite rapidly (in 15 to 20 minutes as reported by Goodwin and Greenhall, 1961).

The three vampires of the Desmodontidae are generally thought of as being obligate blood-feeders, with the exception of occasional instances of insect-feeding by *Desmodus*. Considering the marked structural and behavioral specialization for blood-feeding in this group, relative obligation to sanguivorous habits appears sufficiently verified. Wimsatt and Guerriere (1962) noted the rather large daily blood meals taken by *Desmodus* in captivity, averaging over 15 ml per day over a period of a year, and Wimsatt (1969) recently confirmed these observations in the field.

Three of the remaining four species (*Natalus, Plecotus,* and *Molossus*) may be considered obligate insect-feeders. Ross (1967) noted that *P. townsendii* is especially fond of small Lepidoptera. According to Pine (1969), *Molossus ater* in Costa Rica takes many small insects, especially ants, other small Hymenoptera, and a variety of beetles. Little information is available regarding the habits of the Natalidae; Goodwin and Greenhall (1961) stated only that the diet of *Natalus* is restricted to insects.

Pizonyx vivesi is presently recognized as a regular fish-eater, although insects and small crustaceans have been observed in quantity in the stomachs of several specimens (Reeder and Norris, 1954). Small sardines and anchovies may comprise a substantial portion of the fish diet of *Pizonyx*.

It is of interest to note that many species of a number of families, although principally restricted to a non-insect diet, occasionally take insects.

Gross Morphological Features

Although variation in general morphology among the species of bats examined is extensive and each species is clearly unique in one or more ways, it is apparent that trends in similarity do exist among both closely related genera and among those with similar food habits. Several broad categories of general structure can be seen in the 13 species examined.

The first of these groups, which includes *Noctilio, Pteronotus, Natalus, Plecotus,* and *Pizonyx,* is characterized by a stomach that is relatively short in relation to breadth, and that has a convex dorsal surface with no dilation of the dorsal surface of the fundic caecum, and is generally symmetrical, with the terminal portion (that region distal to the gastroesophageal junc-

tion) equal (or nearly so) in length to that of the fundic caecum. Also, the terminal stomach is relatively short and never sharply recurved craniad, and the esophagus enters the stomach approximately midway along the lesser curvature, never at a marked angle to the stomach. Two additional vespertilionids, *Myotis velifer* and *Antrozous pallidus* (both insect-feeders) examined by Rouk (1968), would seem to fit this category. This simplified, tubular gastric form is restricted to, although not universal among, carnivorous species. *Pizonyx vivesi* deviates most from the basic plan discussed, because its esophageal entrance is slightly angled and its stomach is considerably more rounded than in the other four genera. The apparent specializations in gross morphology observed in *Piznoyx* cannot be attributed necessarily to fish-eating, however.

Generally speaking, the stomachs represented by this first group of bats closely resemble those of the Insectivora discussed by Myrcha (1967) and by Allison (1948). This similarity is greatest between bats (excluding *Natalus*) and hedgehogs of the family Erinaceidae, with which there is striking correspondence in configuration and relationship of the fundic, pyloric, and gastroesophageal areas, as well as similar distribution of gastric mucosa. *Natalus,* with its relatively straight pyloric tube, most closely resembles soricids. It is suggested that this first category of species is represented by those with stomachs that topographically and grossly resemble the probable simple primitive condition in bats, species with a more specialized fundic caecum and an elongate terminal portion being most advanced. This statement is not intended to infer that the stomachs are necessarily primitive in all characteristics, but only that the basically simple "insectivore-type" prevails.

Two species of obligate insectivorous bats included in this study clearly do not conform to the category described above. While distinctively tubular and convex throughout on the dorsal surface, the stomachs of *Rhynchonycteris naso* and *Molossus ater* have notably elongate terminal portions in comparison to those of the five species previously discussed, as well as a sharply angled entrance of the esophagus into the stomach. Pyloric recurvature is moderate in *Rhynchonycteris* and pronounced in *Molossus;* regarding topography, these two species represent a second category of more specialized insectivorous kinds. Possibly they are adapted for consumption of relatively large quantities of food during a single feeding, resulting in extended exposure to proteolytic digestion in the elongated pyloric portion of the stomach. It will also be noted that the transitional zone from fundic to pyloric mucosa is most extensive in these two species among all those examined with elongated terminal portions. This condition would tend to expose the food bolus to HCl-producing mucosa for a greater distance than in other species. A more complete analysis of quantities of food consumed is required to verify this suggestion.

A third group, which includes *Carollia perspicillata, Sturnira lilium,* and *Artibeus lituratus,* have stomachs with a moderately to extensively developed cardiac vestibule, well-developed fundic caecum that is dilated and hooked on the dorsal surface, and a narrow, elongate terminal portion that is recurved sharply craniad. Notable related specializations of the stomach wall are discussed in preceding sections. The conditions prevailing in these species would seem to relate to accommodating large quantities of bulky food material, consistent with the frugivorous habits of these species. The specializations of, and general increase in size of, the fundic caecum in frugivorous bats would seem to parallel a similar trend noted by Vorontzov (1960) in passing from primarily albuminous (animal) to principally cellular (plant) feeding in muroid rodents. A chamber-like cardiac vestibule, especially well developed in *Sturnira* and *Artibeus,* increases the available surface to which ingested material is exposed in the gastric phase of digestion. It is not possible at this time to conclude whether the vestibule is to be considered histogenetically a portion of the esophagus or a dilated portion of the lesser curvature, although in light of the well-developed gastric mucosa within the vestibule the latter explanation seems the more probable. As noted previously, *Carollia perspicillata* may be a less obligate fruit-eater than either *Sturnira* or *Artibeus* and some features of gross morphology that tend to distinguish *Sturnira* and *Artibeus* from remaining kinds are, indeed, partially reduced in *Carollia.* The cardiac vestibule is distinctive as a conical ampule externally in *Carollia,* although noticeably shorter and relatively narrower than in either of the other two species. The fundic caecum is well developed and dilated dorsally, although somewhat more rounded as in *Glossophaga,* a species to be discussed shortly. The pyloric sphincter of *Carollia* combines features observed in *Artibeus* (such as being long and symmetrical) with a structural feature of insectivorous or partially insectivorous kinds in which the sphincter valves increase in breadth toward the inner limit (narrowly tapered in *Artibeus* and reduced to a vestige in *Sturnira*) and terminate in a broadly rounded apex. *Carollia* clearly is a species that normally consumes mostly pulpy plant material and fruit juices, but perhaps has turned to such habits only relatively recently inasmuch as its stomach appears intermediate in many ways between insectivorous and frugivorous types.

The fourth category of stomachs represented by those of *Phyllostomus discolor* and *Glossophaga soricina* suggests an additional type of intermediacy between strictly herbivorous and carnivorous conditions. The cardiac vestibule is either reduced to a vestige (*Phyllostomus*) or absent (*Glossophaga*), and, whereas the fundic caecum is dilated and expanded on the dorsal surfaces, the caecum appears relatively smaller in comparison to the remaining stomach than in the two obligate fruit-eaters discussed

previously. Only short endpieces of the terminal portions are recurved cranially in both *Phyllostomus* and *Glossophaga,* although the terminal tubular stomach is extensive in both. Also, whereas the pyloric sphincter retains its narrowness, as observed in other phyllostomatids, the valve in these two species is asymmetrical (larger on the greater than the lesser curvature). It is suggested that asymmetry of the pyloric sphincter is in some way related to carnivorous feeding in bats (additional discussion on this point follows in a more detailed comparison of the pyloric sphincters examined). In addition, the stomachs of *Glossophaga* and *Phyllostomus* appear to be "intermediate" in degree of symmetry, revealing more gradual antero-posterior curvature than observed in *Carollia, Sturnira* or *Artibeus.* The significance of such general arching of the stomach is obscure, although an hypothesis regarding the function of sharp recurvature of the pylorus is presented below.

In *Sturnira* and *Artibeus,* which presumably consume rather large quantities of bulky plant material, mechanisms to retard gastric emptying, thus exposing food material that is difficult to digest to longer periods of gastric enzyme exposure, would theoretically be of selective advantage. Such mechanisms are well known in other kinds of herbivorous mammals (for example, ruminate and semi-ruminate stomachs of bovines and many herbivorous rodents). A sharply angled pyloric tube such as found in *Artibeus, Sturnira* or *Carollia* likely would have a distinctive crook at the point of recurvature when the stomach is filled to the point of distention. This crook in the terminal stomach might well help to retard the rapid transport of food through the stomach. A single insectivorous species, *Molossus ater,* was found to have a similarly sharp cranial recurvature, although the terminal recurved endpiece is extremely short, and the degree of constriction of the pylorus upon complete distention of the stomach with food is probably not great. It is apparent that the degree of recurvature of the pyloric portion of the stomach is to some degree a function of angulation of the stomach with respect to a transverse plane through the animal (that is, the more anteriorly displaced is the fundic caecum, generally, the greater the pyloric bend). In the case of the extremely large and elongate stomach of *Molossus ater,* apparent compensation for size has been made by a shift of the stomach up and to the left, underneath the left lobe of the liver. Thus, the degree of pyloric recurvature is also, most probably, a function of relative size of the stomach; large stomachs may be the result of increased nutrient requirements or reduced energy per unit of food or both. Members of the family Molossidae are strong, fast fliers, which represent the most advanced development of the forelimb for flight among bats. Superior development of flight allows at least one species, *Tadarida brasiliensis,* to migrate, and the relatively large size of the stomach in this

species (Rouk, 1968), to accommodate relatively large amounts of food, is not surprising in this regard.

It would appear then, that elongation of the stomach is related to increased food intake in the evolutionary history of the Chiroptera. An interesting parallel in this regard can be found in the Insectivora. Myrcha (1967) has found that the stomachs of some insectivores, notably Soricidae and Talpidae, reveal elongation of the terminal portion of the stomach, likely also in response to increased food requirements.

The last category to be considered, containing only *Desmodus,* represents the vertex of specialization in gross gastric morphology in bats thus far examined. It is difficult to observe any major feature of the stomach of *Desmodus* that closely resembles the condition in any other species thus far studied (excluding, of course, *Diphylla* as discussed by Grassé, 1955). The elongate and tubular fundus is clearly adapted to hold relatively large amounts of blood. Extremely elastic bands of thin, loose, bundled, musculature and distinctive complements of loose areolar connective tissue allow extensive expansion of the fundic caecum. The extremely close proximity of the cardiac and pyloric orifices (Fig. 33) suggests, in the absence of apparent structural modifications of the cardia to assure passage of ingested blood to the left into the caecum, that the pyloric sphincter must be at least partially functional, or as suggested by Selkurt (1966), localized contractions of the proximal area of the duodenum may provide the means of gastric closure at the lower end. The pyloric sphincter is extremely thin, symmetrical, and appears to be structurally most similar to that in several phyllostomatids, especially *Carollia* and *Artibeus;* in *Desmodus* it is reduced secondarily to a thin flap.

The long, thin, tubular nature of the stomach of *Desmodus* undoubtedly serves to facilitate utilization of a wholly liquid meal in several ways. Elongation of the stomach coupled with extensive vascularization of the submucosa provides increased surface area for the rapid absorption and excretion of fluids as noted by Wimsatt and Guerriere (1962). Modifications of the gastric mucosa, to be discussed later, may also provide for increased surface area. The tubular stomach, when folded on itself midway along its length and displaced longitudinally or transversely within the body cavity, would provide a mechanism for balancing the extremely large blood meal equally on the left and right sides of the bat, providing for more stable flight from the host after feeding. Vampires have been observed to engorge themselves to the point that they are unable to take flight after feeding (Goodwin and Greenhall, 1961); a means to provide a "balanced load" would seem to be advantageous to these bats. Studies of the intravisceral configurations of the stomach of *Desmodus* just after feeding should be carried out to test this suggestion.

TABLE 2. Classification of pyloric sphincters of several species of bats.

Valve flaps absent	*Sturnira*
Valve flaps present, broad (apex blunt)	
short, nearly symmetrical	*Pizonyx*
short, asymmetrical	*Natalus*
long, asymmetrical	*Noctilio*
	Plecotus
	Molossus
	Rhynchonycteris
Valve flaps present, narrow	
short, symmetrical	*Desmodus*
long, symmetrical	*Carollia*
extremely long, tapering, symmetrical	*Artibeus*
long, asymmetrical	*Pteronotus*
	Phyllostomus
	Glossophaga

Extensive variation in morphology of the pyloric sphincter in bats (Table 2) presents an interesting physio-morphological problem. Without exception, every species of carnivorous or partially carnivorous bat examined in this study revealed some degree of asymmetry of the pyloric sphincter (that is, the valve was not uniform in length or breadth, or both, throughout the circumference of the gastroduodenal junction, the larger portion of the valve usually being on the greater curvature). This asymmetrical condition is in contrast to the pyloric sphincters of herbivorous and sanguivorous species, which, although highly variable in length among species, are equal throughout their circumference within a given bat. Dearden (1969) examined the pyloric sphincters of four genera of microtine rodents, noting two types of asymmetry in the sphincter—that in which the larger sphincteric mass was on the greater curvature, and conversely, that in which the valve was larger on the lesser arc. Dearden suggested that in those species of voles with the greater mass of muscle on the greater curvature, sphincteric action would seem to be of a milking nature, whereas symmetrically circular closure would likely result from the other condition. Although a well-developed membrane of gastric mucosa comprises an important part of the pyloric sphincter in bats, which lack the pediculated squamous flaps apparently important to the closure mechanism in some species of voles, the anatomical variability observed in pyloric sphincters in bats suggests that these mammals also have functional differences in gastroduodenal closure mechanisms. A relatively effective gastroduodenal closure mechanism, such as would theoretically be produced in those species examined with symmetrical sphincters (*Sturnira, Artibeus, Carollia, Desmodus*), would presumably be of greatest advantage in bats feeding on materials that are difficult to assimilate, such as pulpy plants and blood. Nothing is known

regarding the physiology of the pyloric sphincter in bats, although conditions in primarily non-carnivorous bats suggest that additional studies on pyloric sphincter morphology and physiology in bats might prove most interesting in relation to feeding ecology.

Fundic Caecum

Comparative examination of the fundic caeca of bats reveals little specialization that can be directly related to feeding habits. An exception is *Desmodus*, in which the entire stomach is essentially a thin-walled caecum adapted to accept and retain a meal of blood that requires no physical breakdown; the complex and normally thick muscular wall observed in fundic caeca of other bats is lacking. No species examined lacked a fundic caecum, and all species (excluding *Desmodus*) revealed fundic caeca that were but slight alterations of a basic plan. All species of the Phyllostomatidae, with the possible exception of *Pteronotus*, possess a fundic caecum dilated at the apex and hooked dorsally to a greater or lesser degree. This feature is restricted to phyllostomatids; it is best developed in *Artibeus*, *Sturnira* and *Carollia*, to a lesser degree in *Glossophaga*. It is reasonable to suggest that this condition is also related to increasing effective gastric volume in those species that consume large quantities of plant bulk and liquid material, being absent (or reduced) in those kinds that have retained (or returned to) insectivorous and carnivorous habits. The fundic caecum of all carnivorous species consists of a simple, usually short, blind, lateral extension of the mid-stomach, excepting the slight terminally hooked apex observed in that of *Phyllostomus* (an omnivore), and functions to hold a portion of the food material during the period of gastric churning.

Cardiac Vestibule

The cardiac vestibule and its probable functional significance in three fruit-feeding or at least predominantly fruit-feeding kinds (*Sturnira*, *Artibeus*, and *Carollia*) has previously been discussed. The vestibule in these three species is unique among those examined in that it represents a nearly distinct gastric entity. It is of interest that fruit-eating megachiropteran bats may have an equally well-developed cardiac vestibule, implying further a relationship between consumption of large complements of fruity material and invasion of gastric mucosa craniad into the lower portion of the abdominal esophagus. All insectivorous and partially carnivorous species, as well as the one sanguivorous species studied, have either a relatively short vestibule or lack one entirely, with the possible exception of *Natalus stramineus*. The vestibule of *Natalus* is rather extensive in breadth, although not as distinctively delimited from the lesser curvature as the vestibule of the three frugivorous species. Although nutritional requirements of insectivorous and carnivorous bats likely are equivalent to, or greater than,

those of fruit-eaters, usable caloric substrate is likely greater per weight of food material ingested. Insect-eating bats macerate their food into fine fragments, and the few carnivorous kinds whose digestive efficiency has been examined have been noted to leave little recognizable animal material other than matted hair and hard fragments in the fecal material, even when whole mice are consumed. This efficiency in the digestive process suggests relatively lower requirements of food mass than in fruit- and blood-feeders; hence, comparatively less modification of gastric proportions are required to increase internal volume and surface area. It is of interest to note that *Natalus,* the single insect-feeder possessing a large cardiac vestibule, also has a relatively small fundic caecum and a terminal stomach that is moderate in length, but extremely narrow. It is probable that the enlarged cardiac portion in this species has developed in response to an otherwise rather limited gastric volume.

Relatively little is known concerning the mechanism of gastroesophageal closure in bats, which is surprising in light of their interesting and almost unique habit among mammals of hanging upside down while roosting (after and sometimes even during the period of feeding). An anatomically distinctive cardiac valve is unknown in bats with the exception of that reported herein for the genus *Noctilio.* This structure evidently has been derived independently in this genus, perhaps in response to the acquisition of fish-eating habits later abandoned by *N. labialis.* The stomachs of both species of noctilionids appear comparatively small in relation to body size, and the unique cardiac valve, assumed functional to some degree as specialization of the mucularis mucosae is apparent, may prevent back-up of large quantities of ingested fish from a relatively small stomach. Should a cardiac closure mechanism exist in other bats, as seems likely, it must be represented by a physiologically specialized muscular component of circular fibers and muscularis mucosae at or near the gastroesophageal junction, perhaps consisting partly of locally thickened musculature as in those species with a prominent incisura cardiaca. Anatomical specialization of muscle layers at the gastroesophageal junction in bats other than *Noctilio* is restricted to a slight breakup of fibers of the muscularis mucosae, the significance of which is unclear, and some notable local thickening of the circular muscle layer just below the gastroesophageal junction in *Rhynchonycteris, Glossophaga,* and *Molossus.* Botha (1958a) examined the mucosal folds in the cardia of an unspecified species of bat, probably an insectivorous vespertilionid, and concluded that the mucosa-lined ridges at the orifice formed a watertight papilla, effectively closing the gastroesophageal junction. It is possible that those species with local thickening of the circular muscle layer in this area (*Rhynchonycteris, Glossophaga,* and *Molossus*) have efficient closure of the stomach, although no physiological evidence is avail-

able to support this point. It will be noted that the three species of frugivores all have extremely thin musculature at the gastroesophageal junction and throughout the cardiac vestibule. This condition does not, of course, dispel the possibility of the existence of an active closure mechanism, although the strength and efficiency of a sphincter may be more limited in these species.

Musculature

The walls of all stomachs examined were composed of an outer longitudinal and inner circular layer, and two extremely thin intra-submucosal sheets of smooth muscle, a pattern which is common to other kinds of mammalian stomachs. Variability between species in corresponding depths of various portions of the stomach frequently was found to be less than variation within a single stomach, especially between tubular and saccular portions of several species.

Most of the species examined revealed some degree of increased thickening of the greater curvature wall, in contrast to that of the lesser curvature. The relative amount of, or specific region of, the greater curvature that shows this condition is, again, quite variable and rarely expressed throughout all of the greater arc, or within both outer layers. In *Phyllostomus, Natalus,* and *Molossus,* the muscular wall is consistently thicker through the greater arc, by virtue of the circular layer, than most of the corresponding wall of the lesser curvature. This condition generally holds for *Pteronotus,* although the terminal portion is only slightly thicker in the greater curvature than in the lesser (hence uniformly shallower than in the lesser arc in the three species mentioned above). The circular layer of the greater curvature wall in *Noctilio* is distinctive in being only slightly thicker than the lesser wall, whereas the longitudinal layer is markedly increased in depth in the medial and terminal portions of the greater curvature.

The stomachs of *Glossophaga, Carollia, Sturnira,* and *Artibeus* all possess some degree of sacculation of the fundic caecum, with a greater or lesser degree of reduction of the muscular wall within this portion of the stomach. The musculature of the greater curvature of the fundic caecum is thicker than the facing wall on the lesser curvature in *Glossophaga* and *Carollia,* whereas these two surfaces are essentially equal in depth and thin throughout in *Sturnira* and *Artibeus.* The terminal pyloric portions in these four bats are always thicker than the proximal wall and generally thickest on the greater curvature, although the difference is not noticeable in *Carollia.*

The functional significance of much of this irregularity in the depth of muscle layers is unclear, although conjectures regarding answers to such questions follow where appropriate. In the absence of any pertinent physio-

logical information concerning gastrointestinal tracts of bats, it is difficult to explain such extensive variability.

It would seem likely that differential muscle development that results in greater masses of circular fibers on the greater curvature would likely be a response to increased food intake, which would demand additional basal support in the gastric sac to accommodate the increase in food mass. Although marked modifications in this condition of differential musculature are found to exist in localized portions of the stomach in many species, most still express the condition, at least in the terminal portion of the stomach. Exceptions to this trend, although rare, do exist and much additional work is needed to clarify the role of these conditions.

Especially in *Plecotus* and less so in *Pizonyx*, some marked uniformity in depths of corresponding portions of the lesser and greater curvatures is apparent. Musculature of the fundic caecum in each of these two species is moderate and uniform in depth, except for reduction at the extreme apex; thickening in the pylorus is pronounced in *Piznoyx* and slight in *Plecotus*. *Plecotus* and *Rhynchonycteris* most closely approach the condition of equal thickness of the muscle wall throughout the stomach among the carnivorous and herbivorous species examined. The muscular wall in the stomach of *Rhynchonycteris* is remarkably uniform, *Plecotus* somewhat less so; all remaining species show some local thickening, usually in the pyloric endpiece. It is suggested that the condition of nearly uniform depth of the stomach musculature in these two species is a relatively generalized condition.

Decrease in depth of the caecal wall is apparent among herbivorous kinds, whereas this region remains deep or even increases in depth over other areas in obligate insectivores and carnivores. It would seem likely that gastric volume is of greater importance in herbivorous kinds, hence loss of musculature in the caecum permits an increase in elasticity. On the other hand, prominent musculature in the proximal portion is of greater advantage to insectivorous kinds in increasing the area over which large, rythmical contractions take place, hence the physical mechanism of gastric mixing. It is interesting that *Phyllostomus discolor*, a probably omnivore, approaches the condition of equal muscular depth throughout the stomach to a greater degree than any other phyllostomatid examined, with only slight and nearly symmetrical thickening in the terminal portion of the stomach: this suggests a retention of generalization in this feature in *Phyllostomus* and perhaps in other phyllostomatines.

Quite localized decrease in caecal musculature at the extreme apex (owing to decrease in depth of the circular layer), as occurs in *Rhynchonycteris*, *Noctilio*, *Phyllostomus*, *Plecotus*, and *Piznoyx*, probably reflects a compromise to obtain increasing flexibility and yet remain the substantial musculature required for gastric mixing in carnivorous bats.

Asymmetrical pyloric thickening, discussed previously, is noted to be widespread among bats examined. Where present this does not necessarily correspond with, nor is it restricted to, those kinds with similar asymmetry of the nearby pyloric sphincter, nor is it correlated with relative size of the sphincter. The significance of this feature remains obscure, and its widespread occurrence suggests that studies of gastric motility and the physiological role of the pyloric sphincter in bats need be undertaken to help resolve these questions.

As regards the outer musculature in *Desmodus,* the extensively bundled fibers within both outer layers provide a suitable mechanism to explain prominent expansion of the stomach to hold the large quantities of blood taken in individual feedings. Some suggestion of increased depth of the greater curvature over that of the lesser curvature is to be found near the gastroesophageal junction in *Desmodus,* the significance of which, as in other bats revealing this feature, remains obscure. Although the bundles of circular fibers are variable in size, the total depth of the outer wall is fairly uniform throughout the fundic caecum in *Desmodus,* suggesting symmetrical expansion of the caecum upon filling. The mechanism to allow extensive expansion is not, apparently, reduction of muscular tissue in depth, but an increase in the elastic portion of the wall by way of increased complements of areolar connective tissue.

An index for determining differences and degree of variability in arrangement of circular muscle fibers was taken to be the extent of bundling of this layer as viewed in a mid-longitudinal section of the stomach. This condition, as observed in mid-longitudinal section, is restricted for the most part to the lateral and lower wall of the fundic caecum, but in some is present up to the medial area of the greater curvature. There are, however, several notable exceptions to this trend. The stomach of *Desmodus,* as discussed previously, illustrates extensive bundling throughout all of the fundic caecum, unique in this regard among bats examined. Most species examined had some degree of bundling of the circular layer in the fundic caecum, usually in the lower portion and within the greater curvature. The only exception to this trend was found in *Natalus,* in which the bundling present in a mid-longitudinal section was a small area just proximal to the pyloric bend. The function of gathering of circular fibers into bundles appears to be a gain in degree of elasticity of the stomach, expressed to some degree in the fundic caecum or greater curvature (or both) of most species, especially the phyllostomatids and *Molossus.* The apparent lack of this feature in the fundic caecum of *Natalus* is particularly interesting in light of the unique feature in this bat of increased muscular depth within the fundic caecum in comparison to the remainder of the stomach. This suggests that the stomach of *Natalus* is relatively non-plastic, with little

capacity for expandability of the fundic portion. Whether or not this condition restricts the relative amount of food consumed in comparison to other species cannot at this time be concluded, but seems unlikely to be the case in light of the rather extensive cardiac vestibule near the esophagus in *Natalus,* providing some increase in gastric volume.

Relatively little reference has thus far been made to the longitudinal layer of the stomach, because it consists of only a thin sheet (in comparison to the overlying circular complement) throughout most portions of stomachs of nearly all of the 13 species studied. However, in at least three species of insectivorous bats (*Pteronotus, Noctilio, Natalus*), representing three distinctive families, the longitudinal layer is prominently developed locally throughout part or all of the fundic caecum. In the case of *Natalus* it is as deep as, or deeper than, the thick circular layer throughout most of the caecum. Where such hyper-development occurs, the longitudinal layer of the caecum becomes several times the depth of the remaining portion of this layer, which as noted is usually extremely thin. Except in *Pteronotus,* the omnivorous *Phyllostomus discolor* reveals the best development of the longitudinal layer among the primarily frugivorous phyllostomatid group, and some correlation between this condition and carnivorous habits in bats seems apparent. An increase in longitudinal muscle fibers would increase the strength of the shortening component for a rhythmical-segmentation contraction, which would presumably increase the effectiveness of mixing caecal contents with that of the midportion of the stomach. This suggestion must, of course, be tested by examining additional species with similar feeding habits, and examining the mode of gastric motility in these mammals.

GASTRIC MUCOSA AND THE GLANDS OF BRUNNER

ORIENTATION OF FOLDS

In general, only two patterns of directional orientation of mucosal folds were observed in the 13 species examined. The first condition, that of longitudinal orientation of parallel folds, was found in the tubular portions of all stomachs irrespective of the feeding type represented. Longitudinal orientation to a greater or lesser degree was also observed in the fundic caeca and cardiac vestibules of all insectivorous species, the omnivorous *Phyllostomus,* the piscivorous *Pizonyx,* and sanguivorous *Desmodus.* Within the non-tubular portions of stomachs of several species (including *Phyllostomus, Glossophaga, Plecotus, Pizonyx, Molossus,* and *Desmodus*), which have mostly longitudinal orientation of folds, there occurs slight to moderate wrinkling (or zig-zag arrangement) of the rugae, although no true interdigitation of the folds is to be found. This condition is lacking in several other carnivorous species, most of which (*Rhynchonycteris* excepted) also reveal relatively thick musculature in the fundic caecum. The condition

of wrinkling of the rugal folds appears related to increased ability to stretch the caecal portion of the stomach. Wrinkling of the mucosal folds provides for additional muscular support in the form of folded sheets of muscularis mucosae to compensate for the extremely dilated outer musculature that would result upon marked distention of the stomach. It is not surprising to find that this feature is lacking in those species with deep caecal musculature, which probably restricts the degree of expansion of the caecum.

The second condition of orientation of mucosal folds is that of transverse anterior-posterior orientation. This situation occurs 1) infrequently among a few species of insectivorous kinds (here found restricted to infrequent, short transverse folds in brief areas of the fundic caecum, usually the upper wall), 2) in the fundic caecum of *Glossophaga* and *Carollia* as narrow transverse ridges along the sides, and 3) in an extreme condition of highly complex, heavily interdigitating ridges in the nontubular fundus of *Artibeus* and to a lesser degree that of *Sturnira.* A possible function of these interdigitating folds, that of helping to secure food materials within the fundic caecum for extended periods of time, has been previously discussed for *Artibeus.* An alternative, or at least supplementary, hypothesis would be to suggest that these folds provide for increased elasticity in addition to the already thin outer wall of the fundic caecum to assist in accommodation of large meals of fruit such as are known to be taken by *Artibeus* and *Sturnira.*

Local Reductions in Mucosal Depth

Two conditions of local modification in mucosal depth in comparison to the remainder of the stomach seem worthy of mention, as they are widespread among the species examined. In the stomachs of all species studied, except for *Carollia* and *Sturnira,* the gastric mucosa is clearly deeper in the lesser than in the greater curvature. This condition does not appear correlated with muscular depth as it is found to exist in species with an hypertrophied wall along the lesser arc and along the greater arc, as well as in species with uniform or nearly uniform muscular depth, and is usually restricted to within the zone of fundic mucosa. Perhaps no relationship exists between mucosal depth and digestive efficiency or strength of the gastric wall, although this seems unlikely. Evidence that the condition is best developed and, therefore, most important in carnivorous kinds is hardly conclusive, and thorough study of these patterns should be undertaken in other kinds of mammals with diverse food habits.

A second condition is that of reduced depth of the mucosa within the fundic caecum in comparison to the remainder of the stomach wall. Generalized reduction throughout the fundic caecum occurs in only one species, *Glossophaga soricina,* whereas localized reduction only at the lateral apex

of the caecum (usually slight) occurs in the stomachs of *Rhynchonycteris, Phyllostomus, Plecotus, Pizonyx,* and *Molossus.* Reduced glandular depth in the caecum is generally the result of reduction in number of all types of cells present, but particularly the zymogenic cells. It would appear that this condition is again part of the general hypertrophy observed in other layers at the apex of the caecum in these species, related to increased local elasticity. The herbivorous species and the insectivorous and carnivorous species with thick musculature within the caecum do not demonstrate this condition of local reduction of mucosal depth. They have other mechanisms for increasing the volume of the caecum or have caeca that are relatively non-elastic.

DISTRIBUTIONS OF TYPES OF GASTRIC MUCOSA

Extensive variation between species and surprisingly little variation within species was found in distribution of most of the types of gastric mucosa. The zone of cardiac glands at the gastroesophageal junction is a relatively narrow band in all species examined, but approaches a condition of being a distinctive element of the mucosa in *Pizonyx vivesi,* unequaled in this feature by any other bat examined. The cardiac glands of *Pizonyx* are extremely large and occupy the entirety of the short cardiac vestibule. These glands are composed entirely of mucus-producing cells, and are presumed to be a source of lubricating substance applied to the food material as it enters the stomach (Bensley, 1903). All species examined possessed at least a few of these glands, but their extensive development in *Pizonyx* suggests that the food consumed by this species requires an especially abundant coat of mucus. Whether the fish consumed by *Pizonyx* present in especially abrasive mass for the stomach is unknown. It is of some interest to reflect on the fact that the greatest degree of specialization at the gastroesophageal junction among bats is to be found in two fish-eating kinds studied, the other being *Noctilio leporinus.* It is indeed apparent, however, that these specializations are of a wholly different order—hyperdevelopment of cardiac glands in *Pizonyx* and an anatomical cardiac sphincter lined with squamous epithelium in *Noctilio.* Although seemingly unrelated anatomically, it can be argued that these specializations produce similar conditions at the entrance of the esophagus into the stomach, that of a smooth or heavily mucus-coated surface. The import of this feature as it relates to fish-eating habits should be investigated further.

Although not unique in spatial distribution within the stomach, the cardiac glands of *Natalus* are large in size and are unusual in that not many occur beneath the stratified squamous epithelium at the extreme upper limit of the cardiac vestibule. These glands are nearly identical morphologically to (and about the same size as) the glands of Brunner in the duodenum of this bat. These two types of glands are also identical in

reactivity to two histochemical procedures for mucins (unique among bats examined). The unique similarity in the two glandular types in *Natalus* should be investigated further. Study of the ultrastructire of these cells, along with those of the glands of Brunner, might provide additional evidence regarding the apparent parallelism in structure, as well as shed light on their poorly understood physiological roles in the mammalian stomach. The pyloric glands are easily distinguished from the cardiac glands in *Natalus* and the marked similarity of the latter to Brunner's glands is indeed unusual.

Myrcha (1967) examined the distribution of zones of gastric mucosa in 27 species of insectivores representing three families. He concluded that the often-observed elongation of the terminal portion in many species was a direct result of increased food consumption, and that an extension of the transitional zone between fundic and pyloric mucosa was a consequence of this elongation. Among the bats studied, general correspondence was found between elongation of the terminal portion and elongation of the zone of transitional mucosa except in the Noctilionidae and Phyllostomatidae. In the latter groups the pattern not only breaks down but shows some reversals of the trend among the included species.

An example of this breakdown may be seen in two obligate insectivorous bats, *Pteronotus parnellii* and *Noctilio labialis*. Both have relatively short terminal portions of the stomach, yet have extremely long transitional zones, apparently developed at the expense of the pyloric mucosa. This pattern becomes further complicated upon examination of the transitional areas of *Phyllostomus* and *Artibeus,* two species with somewhat elongate terminal portions, yet extremely narrow transition zones. The distribution of pyloric mucosa may be an important controlling influence in determining the amount of pylo-fundic transitional mucosa present in bats, because those species with extremely broad transitional zones (for example, *Rhynchonycteris, Noctilio,* and *Pteronotus*) have small complements of pyloric mucosa, and, conversely, those species with extremely narrow transitional zones (for example, *Phyllostomus, Artibeus,* and *Pizonyx*) have rather extensive regions of pyloric mucosa, as compared with their closest relatives. It is thus apparent that the phenomenon of coelongation of the terminal stomach and zone of transitional mucosa, as outlined by Myrcha (1967) for the Insectivora, is not found among the frugivorous Microchiroptera. Specific information concerning the relationship of feeding habits to the physiological significance of the pyloric mucosa is needed to help resolve this question.

The gastric glands of bats are, for the most part, similar to those of other kinds of mammals in types of cells present and in the distributional order of cells within the tubules from one end to the other. However, the

proportion of individual tubules occupied by various types of cells, and the depth of various mucosal and submucosal layers differ from the arrangement in many other mammals. The gastric glands generally may be regarded as shallow in comparison to those of rodents and insectivores, animals of similar size. The cause or effect of the shallow nature of these glands appears primarily to be a loss of parietal and mucous neck cells in medial areas of the tubules. The result of this loss is greater equality in length among regions occupied by zymogenic, parietal, and mucous neck cells in bats, because the zones of parietal and mucous neck cells tend to be much longer in rodents, insectivores, and many other mammals with a mucosal membrane. In addition, there is a corresponding reduction in the amount of submucosal connective tissue throughout much of the gastrointestinal tract of bats, resulting in a presumably highly elastic intestine and equally elastic local areas of the stomach.

As regards the distribution of pyloric mucosa, no clear-cut patterns emerge with respect to similarities among species with similar food preferences. It is evident however, that frugivorous leaf-nosed bats, as well as the omnivorous *Phyllostomus,* tend to have extensive complements of these glands, with rather narrow transitional zones. This condition, although much less apparent, is found also in *Pizonyx.* Only *Natalus* among the insectivorous bats examined has pyloric glands in an unusual length of the stomach. Because pyloric glands histogenetically represent a type of gastric mucosa in which the cells responsible for secretion of materials engaged in, or complementary to, proteolytic breakdown are replaced by mucous producing types, it is understandable that these highly active digestive cells are less widespread in distribution in frugivorous bats. Several species of carnivorous bats (*Rhynchonycteris, Pteronotus,* and *Noctilio*) reveal a near loss of true pyloric glands with marked proximal expansion of parietal cells toward the pyloric sphincter. A consequence of the elongation of the stomach in frugivorous species has been an extension of the pyloric zone only, rather than corresponding expansion of the transitional zone as seen in most insectivorous kinds. *Phyllostomus* has acquired a stomach configuration and muscular wall more like those of carnivores, and yet, has retained the zonation of gastric mucosa most often observed in frugivorous species. The rather extensive distribution of pyloric mucosa in *Natalus,* the stomach of which is unusual in many features, is unique among insectivorous species examined, a probable consequence of notable elongation of the terminal portion. *Glossophaga,* an apparent "intermediate" in the true sense of the term, more closely approaches the "insectivorous" condition in distribution of pyloric and fundic mucosa than does *Phyllostomus.*

These conclusions do not refute the possibility that relatively numerous pyloric glands at the proximal end of the stomach may be of some con-

siderable physiological advantage in one or more of the bats studied, particularly the frugivorous species in which they are so abundant. Numerous physiological roles have been suggested for the mucous producing cells of these glands, including their being sites of anti-autodigestion enzymes and neutralizers for pepsin among other things. However, until the exact physiological role of these glands is understood, it is difficult to draw meaningful conclusions regarding their relative abundance in the stomachs of bats.

Fundic Mucosa

The fundic mucosa comprises the most morphologically specialized and presumably the most physiologically specialized portion of the gastric mucosa in bats. Fundic glands always occupy the majority of the internal surface area of the stomach and are characterized by the presence of both parietal and zymogenic cells within the tubules. That portion of the gastric mucosa that contains numerous parietal cells but no zymogenic cells is here not considered fundic, but rather transitional mucosa, mostly for the sake of convenience. It is therefore to be assumed that when distributions of parietal cells in the stomach as a whole are considered, the transitional mucosa is included as a part of these distributions.

The zymogenic cells are considered to be the site of secretion of the enzyme pepsin, activated to proteolytic action in the presence of HCl. Although the greatest numbers of chief cells were found in several insectivorous species, other insectivorous and carnivorous bats revealed smaller complements of chief cells than did frugivorous species. There is no clear relationship, therefore, between food habits and relative numbers of zymogenic cells. The substantial reduction in the number of these cells in *Desmodus* is taken to be a consequence of general hypertrophy of fundic glands in this bat. The striking depletion of zymogenic cells and especially parietal cells in *Desmodus* elicits interesting questions concerning the ability of *Desmodus* to assimilate food material, particularly in light of the high percentage of solids found to be utilized metabolically by *Desmodus* (Wimsatt and Guerriere, 1962).

It is clear that wherever zymogenic cells are notably abundant, the distribution of parietal cells is correspondingly limited to a narrow portion of the tubule. The relative proportion of the gastric tubule occupied by chief cells seems to be a stronger controlling force affecting the numbers of parietal cells present than the varieties of foods taken in the diet. Frugivorous, insectivorous, and piscivorous species were observed with both restricted and extensive complements of parietal cells in the fundic and transitional areas. Such extensive variation remains unexplained. Allison (1948) has suggested that distribution and numbers of parietal cells may remain static in the gastric mucosa of insectivores, and Rouk (1968) observed no dif-

ferences in the distributions of parietal cells in active and hibernating *Myotis velifer*. These facts suggest that differences between species in complements of at least some cell types in the gastric mucosa is, in all likelihood, real and definable interspecific variation, the significance of which requires additional investigation for adequate explanation.

It will be noted that in three species examined (*Rhynchonycteris, Noctilio,* and *Pteronotus*), nearly all of the gastric mucosa contains some parietal cells and these cells are, for the most part, extremely small and numerous. Perhaps large numbers and extensive distribution of parietal cells in these species compensates for small cell size to provide the needed concentration of HCl.

As in the case of zymogenic cells in bats, no clear-cut patterns emerge with regard to relative abundances of parietal cells in comparison to types of foods taken. The especially numerous parietal cells found to occur in *Artibeus* may be related in some way to the rapid food transport in this species, with a substantial flow of HCl being required to counterbalance the presumed short exposure to digestive fluids. This conclusion is only a supposition and requires further analysis. It may be that parietal cell abundance is related to rate of food passage in other species, or that the abundance of other cell types in the gastric mucosa is also related to time of exposure of the food to gastric digestion, although little information is available on this subject.

With the exception of *Artibeus,* in which the parietal cells are both abundant and of large size, there is a trend among the bats examined to suggest that these cells are relatively large in species in which they are few in number; conversely, the cells are smaller in those bats in which they are more numerous. To my knowledge, no such suggestion of an inverse correlation between size and abundance of parietal cells is to be found for any other kind of mammal. It is of interest to note that Allison (1948) observed the parietal cells of species of the Insectivora to be progressively smaller from the lower to the upper boundary of their distribution within an individual fundic tubule, a condition found to occur only in *Rhynchonycteris* among the 13 species of bats examined herein. At least 10 of the remaining 12 species (the condition is unclear in *Carollia* and *Desmodus*) revealed the reverse situation—the largest cells were toward the surface of the mucosa. The parietal cells closest to the surface of the gastric lining are presumed to be the "oldest." Differences in growth capacity and physiological activity in parietal cells in various species of bats, as well as between major subgroups of mammals, seems probable.

It is apparent that greater local variation within the stomach in distribution of parietal cells and zymogenic cells, as well as in depth of gastric pits, is found among insectivorous or partially insectivorous bats as a group,

but not among frugivorous, piscivorous, or sanguivorous kinds. The fundic mucosa of insectivorous kinds is consistently better developed in the lesser curvature than in the greater curvature; in terms of development longitudinally it usually reaches its maximum within the middle portion, decreasing in richness of cell types in either direction laterally. The reduction within or at the apex of the fundic caecum in many species appears also to be related to increasing the elasticity of the stomach wall.

Few comments have thus far been made specifically regarding relative amounts of gastric mucus produced via the combined secretions of pyloric and cardiac glands, surface epithelium, cells of the gastric pits, and the deeper mucous neck cells. Considerable variation exists among species in depth of the surface epithelial layer, as well as depths of the gastric pits within the fundic mucosa. Those species with relatively deep gastric pits or particularly thick surface epithelium might theoretically produce the most epithelial mucus. The three primarily frugivorous species of the Phyllostomatidae along with *Phyllostomus* have both extensive pyloric mucosa and relatively deep surface epithelium, suggesting some probable advantage to abundant mucous secretion in relation to frugivorous habits. The surface epithelium of *Glossophaga* is comparable in depth to most insectivorous species. The extremely well-developed gastric epithelium of *Desmodus* may be traceable to its close phylogenetic relationship with the Phyllostomatidae; however, it is most likely related in some way to the extensive capacity for absorption of water from the stomach into the vascular network, as comparatively little surface mucus was observed in *Desmodus* in histochemical tests for mucopolysaccharides.

The gastric pits of the fundic tubules, formed by an apparent involution of the surface epithelium, are unusually well developed in *Phyllostomus*. This feature, in combination with the extensive complement of deep, massive pyloric glands and notably thick surface epithelium, presents *Phyllostomus* as an unusually heavy producer of gastric mucus. The extensive quantities of food known to be consumed in rather short periods of time by species of *Phyllostomus* would demand high levels of enzyme and acid. Rather complete decomposition of materials such as bone (Dunn, 1933) must produce gastric environments that threaten the mucosal lining unless a deep mucous coat is present. Finally, as regards gastric mucous production, several species had differential increase in the depth of the gastric pits within the fundic caecum in comparison to the remainder of the stomach. This increase is most often accompanied by corresponding reduction in numbers of other cell types in these glands; the advantage of having relatively more surface mucus in this area than in the remainder of the fundic portion is unclear.

There exists a trend among certain groups of mammals for a relatively

greater distribution of the glands of Brunner in the upper duodenum of herbivorous species as opposed to carnivorous species. However, an impressive group of exceptions to the trend may be found without exhaustive search, as in bats. One general statement regarding the distribution of these submucosal glands in bats can be made: these highly convoluted elements are always restricted to the immediate vicinity of the pyloric sphincter, usually in a small mass, with little or no representation in the form of smaller, isolated clumps inferior to the main mass, as is common in other kinds of mammals. Some variation exists, however, in relative distribution of these glands among bats, in the morphology of glands, and in at least two species in degree of abundance in the terminal portion of the stomach. Two of the three frugivorous species, *Artibeus* and *Carollia,* have Brunner's glands so reduced in distribution as to be nearly lost; those of *Sturnira* are only moderate in abundance in the duodenum, although they are extensive in the pyloric stomach proximal to the pyloric sphincter (shared apparently only with *Molossus*). Among the phyllostomatids examined, the greatest masses of Brunner's glands were observed in *Pteronotus* and *Phyllostomus,* two species that likely consume insects in quantity. As the functional role of secretions of Brunner's glands remains obscure, it is difficult to comment on the meaning of variation in their distribution. It would appear that certain frugivorous kinds have secondarily lost most of these glands. Carleton (1935) noted that the location of the common bile or pancreatic duct in some mammals may determine the limit of distribution of Brunner's glands into the duodenum, although there are exceptions. The common bile duct enters the duodenum only a few millimeters distal to the pyloric sphincter in bats, and may be related in fact somehow to distribution of the glands of Brunner. However, it must be noted that in *Molossus* the glands occur slightly beyond the entrance of the common bile duct into the duodenum, and, in fact, an ampulla is formed at the junction as a result of invasion of Brunner's glands into the duct. The general consensus now is that the glands of Brunner function to protect the lining of the initial portion of the duodenum from the damaging action of acid material escaping from the stomach (Grossman, 1958). In this respect, the near loss of Brunner's glands in a species such as *Artibeus* with its rather extensive number of large parietal cells is indeed perplexing. The invasion of the glands into the pyloric portion of at least two distantly related species, the food habits of which are entirely different, suggests that this condition might be widespread among certain families. Probably it confers additional protection against damage to the pyloric mucosa of *Molossus* and also especially to *Sturnira,* although the particular need for such a mechanism in these species is not readily apparent.

In concluding the discussion of gastric structure in relation to feeding,

it seems appropriate to suggest that control over morphology may be two-fold, one factor affecting the general shape and relative proportions of various regions of the gastric sac and the other controlling the distribution and abundance of elements of the gastric mucosa. Each factor acts separately in gastrointestinal evolution to accommodate particular types or quantities of food. In this regard, it appears that the quantity of food consumed may be an especially important criterion in the evolution of gastric structure. Elongation of the stomach has been a particularly important event in the acquisition of frugivorous habits in bats, whereas most insectivorous and all piscivorous species examined have retained a relatively simplified stomach. Those species thought to be non-obligate feeders and that take substantial quantities of both animal and plant matter, were found to be somewhat intermediate in the structure of the stomach. Gastric structure as observed in bats does not usually correspond with the conditions found to exist in the Insectivora, although *Natalus* and *Rhynchonycteris* closely parallel the Insectivora in several features. In general, evolution away from insectivorous feeding in bats has resulted in noteworthy specialization in one or more structural features of the stomach.

SYSTEMATIC RELATIONSHIPS AS REVEALED BY GASTROINTESTINAL STUDIES

Although the stomach of each of the 13 species examined was clearly distinctive in one or more major features, clear-cut relationships were found within families as well as among closely related families. Modification of gastric structure to accommodate and assimilate foods other than insects has led to marked changes in external configuration of the stomach. Upon further investigation, however, various features of internal gastric structure emerge to reveal more precisely, relationships among various groups of bats. Because the Phyllostomatidae represents the family with the most genera examined, and also has the greatest intrafamilial variability in food habits of included species, it presents the most interesting body of information.

Relationships of bats with the Insectivora, both phylogenetic and as regards food habits, bring to mind consideration of which species of bats, if any, seem to conform most closely to gastric structure as presently known for the Insectivora. The stomach of *Natalus stramineus,* as noted previously, closely resembles those of soricid insectivores in stomach configuration, distribution of mucosal elements, and particularly in external and internal morphology of the terminal or tubular portion. In addition, the stomachs of *Rhynchonycteris* and *Plecotus* also are generalized externally and internally and are strikingly like those of several talpid and erinaceid insectivores, respectively. These relationships suggest a generalized condition in early

chiropterans, most, if not all, of which were probably insect-feeders. The specializations observed in other insectivorous bats such as *Molossus* and *Noctilio* are modifications of the relatively primitive plan seen in the Vespertilionidae, Natalidae, and Emballonuridae.

Within the Vespertilionidae, all species thus far examined reveal marked symmetry of the stomach (esophageal junction located nearly midway along the lesser curvature) and a short, slightly recurved pyloric tube. The list of examined species showing these features includes *Myotis velifer, Plecotus townsendii* (plus the unnamed species of *Plecotus* discussed by Fischer, 1909), *Antrozous pallidus,* and *Pizonyx vivesi.* Eisentraut (1950) included a drawing of the stomach of *Eptesicus serotinus* that, although appearing somewhat distended as do most of the stomachs illustrated by that author, is in general correspondence with those of other vespertilionids. *Pizonyx* and *Antrozous* represent the greatest deviants from the basic plan of overall stomach configuration. The stomachs of both are more rounded than those of other vespertilionids, and *Pizonyx* differs further in its atypical distribution of mucosal zones. Hence, *Pizonyx* is even less like *Myotis,* with which it recently has been merged on the basis of karotypic evidence (Baker and Patton, 1967) than the other vespertilionid genera that have been studied.

The stomach of *Natalus stramineus* is much like that of *Plecotus townsendii* in general topography and in distributions of zones of gastric mucosa, but differs in degree of elongation of the pyloric tube and cardiac vestibule. It is difficult to determine whether similarity in structure is due to parallel adaptation to similar feeding characteristics or close phylogenetic association, or both. It has been suggested that the Natalidae may be systematically closely associated with the vespertilionids through the genus *Kerivoula* (see Dobson, 1878, for a discussion of relationships), and the results of gastrointestinal studies support, to some degree, the contention of close relationship between the two families.

Although highly variable among themselves, the genera of the Phyllostomatidae examined have several features in common that tend to distinguish them as a group from the other families considered in this study. In all species examined, the muscular portion of the pyloric sphincter tends to be narrow in relation to size of the stomach, or may be partially lacking (*Pteronotus*) or nearly completely lost (*Sturnira*). An extremely narrow sphincter was also found to occur in *Desmodus.* Also among phyllostomatids, with the possible exception of *Pteronotus,* there occurs some degree of dilation of the dorsolateral terminus of the fundic caecum, although this expansion is not restricted to the dorsal surface.

Recent investigations of the systematic relationships of the nominal subfamilies Stenoderminae and Sturnirinae have led most investigators to the conclusion that *Sturnira* should be considered a stenodermine. The

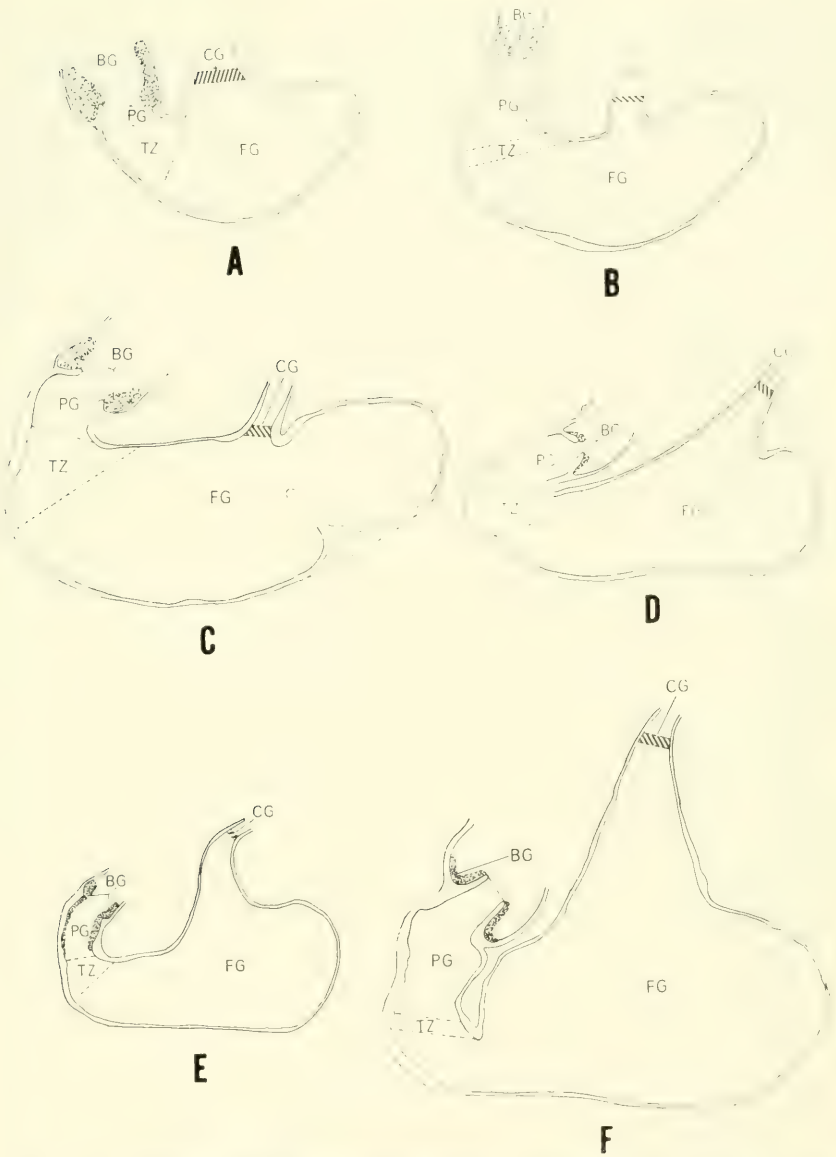


FIG. 53. A diagram illustrating the gradual increase in specialization in stomachs of some phyllostomatid bats. *Pteronotus parnellii* (**A**); *Phyllostomus discolor* (**B**); *Glossophaga soricina* (**C**); *Carollia perspicillata* (**D**); *Sturnira lilium* (**E**); *Artibeus lituratus* (**F**). Stomachs are drawn to scale.

results of my gastrointestinal studies strongly support the proposal that *Sturnira* should be placed in the Stenoderminae.

In addition to the specific features that tend to group the phyllostomatids (including the Desmodontinae), it is also of interest that certain genera in the family resemble one another or a representative of another family in unique ways. As noted, the stomachs of *Artibeus* and *Sturnira* (Fig 53) are similar, resembling each other in gastric morphology to a much greater degree than either resembles representatives of the other subfamilies studied. Additionally, *Phyllostomus* and *Glossophaga* are notably similar, whereas *Carollia* is more or less intermediate between this pair and the previously discussed pair, possibly resembling *Glossophaga* more than the other genera. The stomach (described by Rouk, 1968) of another glossophagine bat, *Leptonycteris sanborni,* closely resembles that of *Glossophaga* in the structure of the terminal portion and differs generally only in the size of the cardiac vestibule (larger in *Leptonycteris*). Although each is specialized in some ways, *Pteronotus* and *Noctilio* are strikingly similar in several features, particularly the distributions of parietal and zymogenic cells, morphology of the gastric glands, and general external topography, suggesting the possibility of closer systematic relationship than has been previously supposed.

A systematic revision of the subfamily Chilonycterinae recently was completed by James D. Smith. The results of my study indicate that this group likely deserves familial recognition, complementing his findings based on other characters.

It is of interest to note that if one arranges six species of phyllostomatids examined (excluding *Desmodus*), each of which represents a presently recognized subfamily according to phylogenetic arrangements such as those of Hall and Kelson (1959), Koopman (1967), or Simpson (1945), there is a gradual transition from insectivorous feeding (*Pteronotus*) to frugivorous habits (*Artibeus*) with variously omnivorous kinds interposed in sequence (see Fig. 53). Corresponding closely with this change in food habits is a progressive alteration of gastric structure from the simplified condition of *Pteronotus* to greater elongation and compartmentalization of the stomach, culminating in the condition found in *Sturnira* and *Artibeus*. Trends in other morphological features complement the trends in specialization observed in stomachs of phyllostomatid bats. The sequence presented in Figure 53 is not intended to imply that one species is necessarily older than another in an evolutionary sense, but that modifications in food habits from the presumed early insectivorous condition have resulted in progressive modifications in the morphology of the stomach as well. The desmodontines are clearly so highly specialized in gastric morphology that it is difficult to relate them to other North American groups, although close relationship with the Phyllostomatidae has been shown by Forman *et al.* (1968) using other characters.

Stomachs of molossids thus far examined reveal that this family consists of relatively specialized insectivorous bats with stomachs that are clearly different from those of other insectivorous species. The stomach of *Tadarida brasiliensis* (examined by Rouk, 1968) differs from that of *Molossus ater* only slightly, containing the same degree of elongation of the terminal stomach and a prominent mid-longitudinal notch in the greater curvature.

The histochemistry of deeper cells of the cardiac and pyloric glands of bats reveals trends difficult to interpret in light of morphological patterns observed; yet the results are of interest with respect to interfamilial relations. It will be recalled that the results of the PAS procedure showed less reactivity within the basal arc or bulbular portion than in the upper, neck region of the cardiac and pyloric glands of all species, except for an equivalent reaction from both glandular areas in the case of *Molossus*. When Maxwell's Alcian blue technique was employed for acid mucopolysaccharides in these glands, the same pattern of differential staining as occurred with PAS was obtained. However, employment of the aqueous Alcian blue (Steedman's method) yielded a similar pattern of results to those of PAS and Maxwell's in all species but *Sturnira* and *Artibeus*, which showed little reactivity at all, and a reversed condition (in which the basal cells in the cardiac and pyloric glands stained considerably darker than the upper cells) in a group including *Natalus, Plecotus, Pizonyx*, and *Molossus*. Although the physiological import of such results is unclear, the consistency of this differential staining in both cardiac and pyloric glands among representatives of the Natalidae, Vespertilionidae, and Molossidae supports the present placement of these families in the superfamily Vespertilionoidea. Winge (1941) suggested that the Molossidae may have arisen from primitive vespertilionids (based on similar structure of the femur and ulna), and the close relationship of the latter group with the Natalidae has been previously discussed. My results suggest that a broader application of more specific histochemical procedures upon the gastric mucosa might prove useful in resolving questions regarding relationships among higher taxonomic categories of bats.

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FRONTISPIECE

Phanaeus vindex MacLeay. Upper left, dorsal view of female; upper right, dorsal view of male. Lower left, lateral view of female; lower right, lateral view of male. (About twice natural size.)

Comparative Skeletal Morphology, Systematics and Evolution of the Phanaeine Dung Beetles (Coleoptera: Scarabaeidae)[1]

W. D. Edmonds[2]

ABSTRACT

The principal purpose of this paper is a re-examination of the supraspecific classification of phanaeine Scarabaeinae based largely upon a comparative study of the skeletal morphology of adults. Part II is a detailed morphological study of *Phanaeus vindex* MacLeay, which was chosen as a "model" species. In this part, which is essentially an independent study of scarabaeine morphology, a terminology is devised which is used in subsequent parts. Part III is an account of the observed variation in skeletal morphology among phanaeines. It is largely upon this variation that the revised classification is based. Part IV is a short resumé of the presumed adaptive significance of skeletal features of phanaeine morphology concerned with fossorial habits. The revised supraspecific classification of phanaeines presented in part V incorporates several significant changes from older systems: 1) the phanaeine genera (not collectively referred to as the subtribe Phanaeina) include *Diabroctis* (=*Taurocopris*), *Sulcophanaeus, Phanaeus, Oxysternon, Coprophanaeus, Dendropaemon, Tetramereia, Homalotarsus* and *Megatharsis; Oruscatus, Gromphas* and *Bolbites* are excluded from "Phanaeina"; 2) two names, *Sulcophanaeus* and *Coprophanaeus*, proposed by G. d'Olsoufieff for subgenera of *Phanaeus* are now used as names of genera quite different in composition from the subgeneric taxa to which the names originally referred; 3) three new subgenera are proposed, *Mioxysternon* for some species of *Oxysternon*, and *Paradendropaemon* and *Coprophanaeoides* for species of *Dendropaemon;* 4) extensive use is made of the informal categories of species-group and species-complex where appropriate in all larger genera. Part VI is a discussion of phanaeine evolution and phylogeny, including generic affinities arrived at by analysis of the taxonomic distribution of derived character states as well as discussions of parallelisms and the evolutionary implications of phanaeine ecology and distribution. Phyletically, the phanaeine Scarabaeinae, which are presumed to comprise a monophyletic group, appear to consist of two distinct phyletic lineages (the *Oxysternon-Phanaeus* and *Coprophanaeus-Dendropaemon* genus-groups), together comprising the bulk of the known species, in addition to a number of small phyletically isolated groups representing relicts of several older phyletic elements.

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PART I: INTRODUCTION

Phanaeines are perhaps one of the best generally known groups of Scarabaeidae. Their striking metallic colors and the often bizarre appearance of "horned" males have made them showy collectors' items for some 200 years. So well noted were they by early collectors that over 80% of all known species (about 90) had been described by 1875. The only serious attempt to date (and a generally very good one) to examine the group *in toto* was made by Gregor d'Olsoufieff (1924), who, in an extensive monograph, provided the first comprehensive keys to species and proposed many new supraspecific groupings.

The primary intent of this paper is a re-examination of Olsoufieff's supraspecific classification of phanaeines based primarily upon the comparative skeletal morphology of adults. Before this could be done critically, however, it was necessary to examine in detail the skeletal morphology of a "model" species to provide a base for the comparative study. *Phanaeus vindex* was arbitrarily selected as this model. Part II of this paper is a treatment of the skeletal morphology of *P. vindex* as well as those aspects of musculature necessary for interpretation of skeletal features. Here a terminology is devised which is used in other sections. Since an effort was made to compare *P. vindex* with other, non-phanaeine dung beetles, this is in effect an independent study of scarabaeine morphology; as such, it is hoped that it will be useful to other students of Scarabaeidae.

Part III is an account of some of the observed variation of skeletal morphology; the conclusions in subsequent parts are based largely upon the data assembled here. Part IV is an examination of the adaptive significance of certain morphological features; although this deals specifically with phanaeines, many of the statements there are applicable to other dung beetles as well. Part V is the systematic section. The concluding section (VI) is a discussion of the evolutionary aspects of phanaeine skeletal morphology, biology and distribution and the bearing of these aspects on their presumed phylogeny.

MATERIALS AND METHODS

The morphological study of *Phanaeus vindex* is based upon examination of both dried museum specimens and specimens preserved in liquid. Like material of *Coprophanaeus lancifer,* a much larger species, was studied simultaneously as a check on several interpretations of the morphology of *P. vindex,* particularly those dealing with muscles. All other material used in this study was dried. For examination of skeletal features, all dried material was first soaked overnight in cold 10% KOH solution. In addition, it was found that the normally much folded hind wings could be extended for easy examination by detaching and soaking them briefly in the same solution.

The majority of the illustrations are line drawings made mostly with the aid

of an ocular grid. Because of the great variation in size of structures, they are not all drawn to the same scale. Photographs are used to illustrate those structures not easily depicted in ink drawings. Efficient illustration of many features requires several views; for orientation in these instances a large, solid dot connects guidelines indicating the *same point* in drawings of the two or more aspects.

Following is a list of abbreviations used in the figures and not defined in captions:

abas2	mesobasalar apophysis
acx	articulation of coxa
afr	apical fringe of labrum
afur2, 3	meso-(meta-)furcal arm
$afur2_p$	lateral process of mesofurcal arm
amcly	anterior margin of clypeus
ampr	antero-median process of labral suspensorium
amt	anterior margin of tentorium
anf	antennifer
ans	antennal socket
ap	aedeagal apodeme
apely	articular process of elytron
apglb	apodeme of glossal bar
apmcly	apical margin of clypeus
$apmm_{1,2}$	apodemes of mandibular muscles
apst	prosternal apophysis
arl	articular line (between clypeus and labrum)
armx	articulation of maxilla
at	acrotergite of abdominal tergum
ata	anterior tentorial arm
atibc	anterior protibial carina
awp	anterior metanotal wing process
ax	axillary sclerite
ba	basalis of mandible
bas2, 3	meso(meta-)basalare
bfur2, 3	base of meso(meta-)furca
br	median brace of mesofurca
bst	basisternum (of prosternum)
bstc	basisternal crest
ca	canthal area
car	cardo
cbr	cephalic brachium
cly	clypeus
clypr	clypeal process
cmb	comb of incisor lobe of mandible
conj	conjunctivus of mandible
cr	transverse tibial carina
cpr	cephalic process
cx	coxa
cxd	coxal depression of sternum
da	dorsal arm of hypopharyngeal suspensorium
dacx3	dorsal articulation of metacoxa
darm	dorsal articulation of mandible
darsgal	dorsal articular sclerite of galea
deye	dorsal portion of eye
dprt	dorsal process of tentorium
dsula	dorsal surface of labrum
ely	elytron
$epim2_{a,l,p}$	mesepimeron (anterior, lateral and posterior surfaces)
epim3	metepimeron
$epim_{pm}$	posterior margin of mesepimeron
epip	elytral epipleuron
epips	epipleural shelf
epis2	mesepisternum
$epis3_{a,l}$	metepisternum (anterior and lateral surfaces)
fcr	fronto-clypeal ridge
fcs	fronto-clypeal sulcus
fe	femur
fet	profemoral tuft
fim	labio-gular fimbria
fla	flagellum of antenna
fs	flexor sclerite of elytron (and hind wing)
fst	metafurcasternum
gal	galea
gl	glossa
glb	glossal bar
glf	glossal flap
gu	gula
gur	gular ridge
gus	gular suture
hl	horizontal lamella of mesonotum
hw	head wall
hyp	hypostoma
imbst	inflexed margin of basisternum (of prosternum)
imepis	invaginated anterior margin of mesepisternum
imgu	inflexed margin of gula
imstn	inflexed margin of sternellum (of prosternum)
inlb	incisor lobe of mandible
ip	interspiracular pad
la	lateral arm of hypopharyngeal suspensorium
lac	lacinia
$lam_{1,2}$	labral muscles
lbpl	labial palp
lcrcly	lateral clypeal carina

lf	lateral file of labrum
lfos	lateral pronotal fossa
llbs	lateral labial sclerite
lobe	postero-ventral lobe of metapleuron
lpc	lateral pronotal carina
lshpx	lateral hypopharyngeal sclerite
mac	mandibular acetabulum
mbfcs	mesal branch of fronto-clypeal sulcus
mbr	median brush of labrum
mcon	mandibular condyle
md	muscle disc of metepisternum
mem	membrane
mgpmt	median groove of prementum
mlhpx	median lobe of hypopharynx
molb	molar lobe of mandible
morg	molar ridges of mandible
mrhpx	median ridge of hypopharynx
mshpx	median hypopharyngeal sclerite
mt	mentum
mth	mouth
mxpl	maxillary palpus
nt_{pi}	posterior inflection of mesonotum
oa	oral arm
ocar	occipital area of parietals
ocfor	occipital foramen
oclb	occipital lobe
ocr	occipital ridge
oes	oesophagus
oford	optic foramen of dorsal portion of eye
oforv	optic foramen of ventral portion of eye
ogs	oculo-gular space
paar	paraocular area of parietals
par	paraocular ridge
pbs	pleurobasisternal suture
ped	pedicel
pfos	posterior pronotal fossa
phb	phallobase
plrg2, 3	meso(meta-)pleural ridge
pls2, 3	meso(meta-)pleural suture
pm	paramere
pmpr	postero-median process of labral suspensorium
pmts	premental sclerite
pntm	circumnotal ridge
pocr	postoccipital ridge
pocs	postoccipital suture
pol	postocular line
polb	postocular lobe
pors	paraoral sclerite
ppha	paraphragmal area of prescutum (of metanotum)
ppl	propleuron
pr	process
prcar	articular process of cardo
prmx	articular process of maxilla
proc	preocular carina
pscu	prescutum (of metanotum)
pstn	metapostnotum
ptbr	posterior tentorial bridge
ptd	posterior tentorial depression
ptibc	posterior carina of protibia
pwp	posterior metanotal wing process
$ph_{1,2,3}$	phragma (first, etc.)
rg	ridge
rmgl	receptacle of mandibular glands
scu2,3	meso(meta-)scutum
sct2,3	meso(meta-)scutellum
sen	sensilla
smt	submentum
sp	scape
spfr	scapal fringe
$ss_{I,II,III,IV}$	stipital sclerite I, etc.
st	stria
stn	sternellum (of prosternum)
sts	mesometasternal suture
$sub3_{ma}$	metasubalar muscle disc
suspx	hypopharyngeal suspensorium
S_{1-8}	abdominal sternum 1, etc.
T_{1-8}	abdominal tergum 1, etc.
tab	metepisternal tab
tar	tarsus
tcrcly	transverse clypeal carina
tib	tibia
tibs	tibial spur
tibt	tibial teeth
topr	tormal process of labral suspensorium
tr	trochanter
trn	trochantin
vacx3	ventral (sternal) articulation of metacoxa
varm	ventral articulation of mandible
varsgal	ventral articular sclerite of galea
veye	ventral portion of eye
vl	vertical lamella of mesonotum
w	w-suture of metanotum
wp2, 3	meso(meta-)pleural wing process
y	articular surface of mesepimeron
z	articular surface of mesepimeron

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PART II: SKELETAL MORPHOLOGY OF *PHANAEUS VINDEX* MACLEAY

This a robust, compact dung beetle common in the eastern United States. The compactness of the body is accentuated by the strong sclerotization of nearly all external surfaces. Compared with related species, *P. vindex* is moderate in size, varying from 14 to 22 mm in length and 8 to 14 mm in width (at the bases of the elytra). Unlike most other scarabaeines, phanaeines are commonly brilliantly metallic in color. In this species most of the upper surface of the head and sides of the pronotum are yellow-green, the remainder of the pronotum is coppery-red, and the elytra, pygidium, exposed pteropleura and greater part of the lower body surface are green to yellow-green.

The sculpturing of the integument varies in nature and degree over the

body surface. In general, the upper surface is strongly rugose; the lower surface is smooth to punctate but never rugose. Vestiture is restricted to pleural and sternal surfaces and to the appendages. Its variation is described below when appropriate.

THE HEAD

HEAD CAPSULE

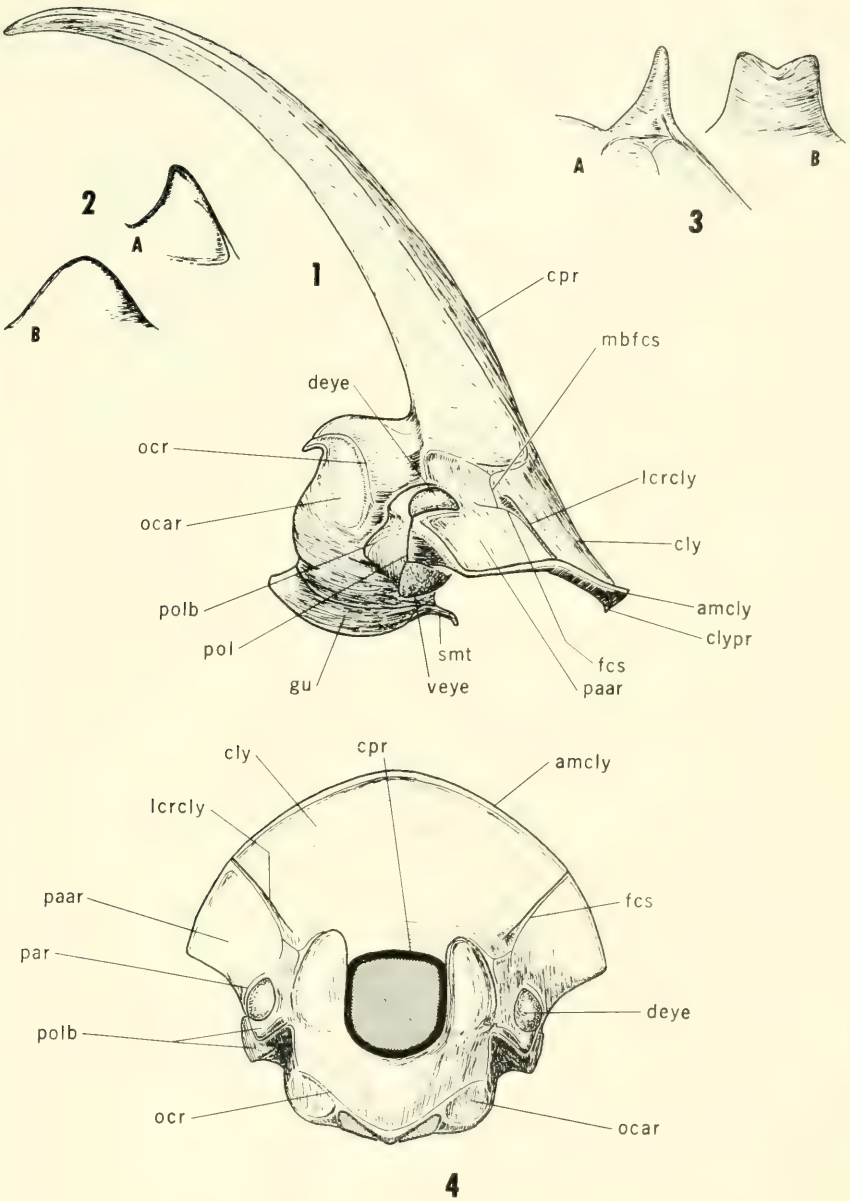
As in other Scarabaeidae, the head is prognathous; the ventral and lateral walls are expanded, bringing the mouthparts into a horizontal plane with their apices directed forward. The capsule is very heavily sclerotized; as is common in beetles, the thickness of the integument tends to obscure many of the surface features (sutures, etc.) observed in other insects.

The most conspicuous feature of the upper surface of the head of large (so called "major") males is a long, massive tapering projection, the *cephalic process* (Fig. 1, cpr), which arises between the eyes and curves posteriorly over the pronotum. The development of the cephalic process (as well as pronotal processes) is allometric and varies considerably within local populations. In smaller ("minor") males, the cephalic process is considerably reduced in length (Fig. 2) or may be nearly absent. The cephalic process of the female, on the other hand, is less variable in development, being a short, erect, apically emarginate projection (Fig. 3). Large, often bizarre corniform outgrowths of the head wall (and pronotum) are very common in the Scarabaeidae, particularly in the subfamilies Scarabaeinae and Dynastinae (see Arrow, 1951).

The flattened, anterior portion of the head dorsum is divided in front of each eye by an oblique *lateral clypeal carina* (Figs. 1, 4, lcrcly) extending from the head margin toward the base of the cephalic process. These carinae are almost always present in phanaeines but seldom in other dung beetles.

Directly posterior and more or less parallel to each lateral clypeal carina is a faint line interpreted here as the *fronto-clypeal sulcus* (= fronto-genal sulcus of authors) (Figs. 1, 4, fcs). Mesally this sulcus curves toward the eye and divides, one short, simple branch continuing toward but not reaching the eye, and the other, Y-shaped *mesal branch of the fronto-clypeal sulcus* (mbfcs) extending toward the base of the cephalic process. Medially the fronto-clypeal sulcus is incomplete. Ventral segments of the fronto-clypeal sulcus (Fig. 9) follow the anterior margins of the antennal sockets and terminate at the dorsal articulations of the mandibles (darm). A medially incomplete fronto-clypeal sulcus with a mesal branch is found in all Scarabaeinae.

The fronto-clypeal sulcus marks an internal *fronto-clypeal ridge* (Figs. 6-7, fcr) joining the head wall above with that inflexed beneath it. Except via a small sinus, the transverse septum thus formed on each side of the head



FIGS. 1-4. *Phanaeus vindex*. **1**, head, lateral view, well developed, "major" male; **2**, cephalic process of "minor" male, A—lateral view, B—frontal view; **3**, cephalic process of female, A and B same as 2; **4**, head of male, dorsal view (cephalic process removed).

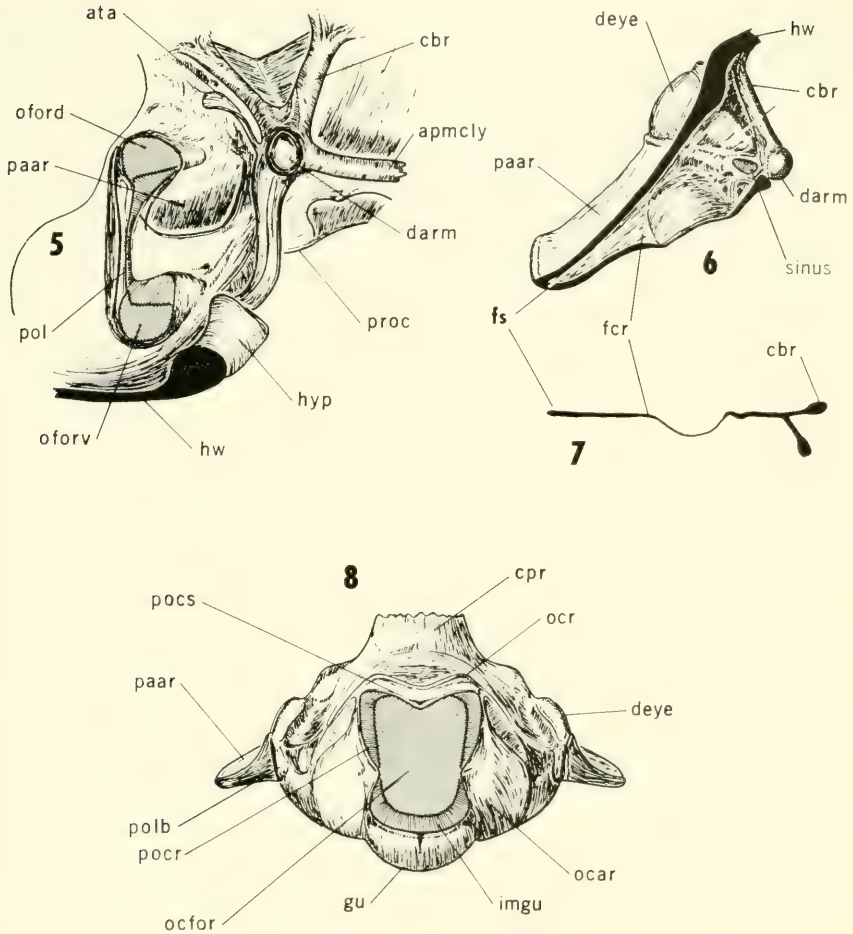
prevents direct flow of hemolymph between the clypeus and paraocular areas of the parietals. The mesal end of each fronto-clypeal ridge forms a dorso-ventral brace between the upper head wall and the dorsal articulation of the mandible. Even though it is *not* an independent structure, for descriptive purposes this mesal bracing portion of each ridge will be called a *cephalic brachium* (head brace). Figure 5 shows the cephalic brachium (cbr). Because its thickened vertical margins resemble two arms extending dorsally from the dorsal articulation of the mandible, the brachium resembles an inverted bipod. Between its "arms" extends a vertical, triangular plate bent along its midline (height) such that a V-shaped line is inscribed where it is fused with the dorsal head wall. This line of fusion follows the arms of the Y-shaped mesal branch of the fronto-clypeal sulcus. The "bipodal" cephalic brachium and almost always coincident Y- or T-shaped mesal branch of the fronto-clypeal sulcus are characteristic of *Phanaeus* and *Oxysternon*. Other phanaeines and non-phanaeines examined have a "monopodal" brachium (see part III, character 7).

Arising directly behind each dorsal articulation of the mandible is a slender, spatulate anterior tentorial arm (Fig. 5, ata). Originating on the expanded distal end of this process is a muscle inserting on the base of the scape. No anterior tentorial pits are visible. The anterior tentorial arms are *very* delicate and highly susceptible to loss if dissection is not careful. Very similar anterior tentorial arms were observed in all beetles examined.

The *clypeus* is greatly expanded and, because of the ventral inflection of its margin, consists of two distinct areas: the flattened *dorsal surface of the clypeus* (Fig. 4, cly), anterior to the fronto-clypeal sulcus above, and the *ventral surface of the clypeus* (Fig. 9), anterior to the ventral portions of the same sulcus. Literature reference to the "clypeus" of dung beetles is usually to the dorsal surface. The dorsal surface of the clypeus of phanaeines is transversely ridged except for a smooth, narrow anterior border (Fig. 79, cly); the ventral surface bears setigerous punctures.

The fold of the clypeus, separating dorsal and ventral surfaces and describing the generally semicircular leading margin of the head is here referred to as the *anterior margin of the clypeus* (Figs. 4, 9, amcly). This margin is slightly upturned and, in *vindex*, slightly truncate or rounded medially. The morphological anterior limit of the clypeus, or *apical margin of the clypeus* (Fig. 9, apmcly), is the U-shaped margin of the ventral surface of the clypeus exposed when the labrum is removed. The *dorsal articulations of the mandibles* (Figs. 5, 9, darm) are spherical condyles at the postero-lateral extremities of the apical margin.

The ventral surface of the clypeus is slightly depressed medially as a distinctly crescent-shaped area which partially receives the labrum. Between this depression and the anterior margin of the clypeus is the *clypeal process*



FIGS. 5-8. *Phanaeus vindex,* male. **5,** eye region of head capsule, internal view; **6,** transverse section through right side of head capsule anterior to fronto-clypeal sulcus (fs=plane of frontal section in Fig. 7); **7,** oblique frontal section of fronto-clypeal ridge; **8,** head capsule, caudal view (cephalic process removed).

(="estructura ventral del clipeo" of Halffter, 1958 and elsewhere) (Figs. 9-10, clypr). The clypeal process of most dung beetles examined is, as in *vindex,* a rather strongly produced transverse carina.

Interpretation of the surface areas of the head immediately posterior to the fronto-clypeal sulcus is difficult. The spatial relationship between the antennal sockets and this sulcus, however, suggests that a distinct frontal region (frons) has been much reduced or eliminated by anterior and/or posterior expansion of other cephalic areas (e.g., the clypeus). Consequently, a vertex

and genae are not distinguishable. These ideas are those of DuPorte (1960); it seems logical to adopt his designation of the dorsal and lateral areas of the head between the fronto-clypeal sulcus and the occipital area as the parietal area, or *parietals*.

The expanded areas of the parietals posterior to the fronto-clypeal sulcus and lateral to the eyes are the *paraocular areas of the parietals* (Fig. 1, 4, 9, paar). Like the clypeus, they are inflected ventrally. Apparently because of their position, these areas are commonly referred to as "genae," a name with doubtful morphological connotations as applied to dung beetles. The paraocular areas of most dung beetles are not "areas," but, rather, each is a finger-like extension of the head wall onto the eye surface. Such a prolongation is referred to as a *canthus*.

In the phanaeines and a few other Scarabaeinae (e.g., *Onitis* and *Scarabaeus*), the paraocular areas of the parietals are expanded *through* the eyes, dividing them completely. Posteriorly each area firmly contacts, but is not fused with, a swelling of the parietals behind the eye, the postocular lobe of the parietals. The line of contact between these two expansions is a vertical "suture" connecting the posterior angles of both portions of the eye; this suture is the *postocular line* (Figs. 1, 5, pol). Figure 5 shows the internal structure of the head capsule of *vindex*, in this region. Here it can be seen that the internal margin of the paraocular area completely divides the optic foramen into upper and lower parts (oford, oforv). This division in *vindex*, and presumably in other dung beetles with similar structure, is correlated with a division of each optic lobe of the brain into two branches, each passing through a separate foramen.

The shape of the posterior margin of the paraocular areas varies among phanaeines. As seen from above in *vindex* (Fig. 4), this margin curves to the posterior angle of the eye. In other phanaeines (e.g., *Diabroctis mimas*, Fig. 115) it extends to the middle of the lateral margin of the eye, leaving, as seen from the side, a vertical flattened area (Fig. 115A, ca) completing the division of the eye. This flattened area will be referred to later as the *canthal area*. It suffices to note here that *vindex* and similar species do not possess a distinct canthal area.

As seen from above (Fig. 4), strong depressions in the dorsal head wall behind the eyes set off the *postocular lobes of the parietals* (polb). These prominent lobes fit into notches in the anterior pronotal margin. Except for the dorsal portions of the postocular lobes which protrude from these notches, the dorsal surface of the head between the postocular lobes and posterior to the cephalic process is concealed by the anterior pronotal margin upon retraction of the head. The cephalic-prothoracic interlocking mechanism achieved by accentuation of the postocular lobes of the parietals and notching of the anterior pronotal margin is characteristic of *Phanaeus*. Although it is

approached in *Oxysternon,* this mechanism is apparently not found in other phanaeines or other scarabaeines.

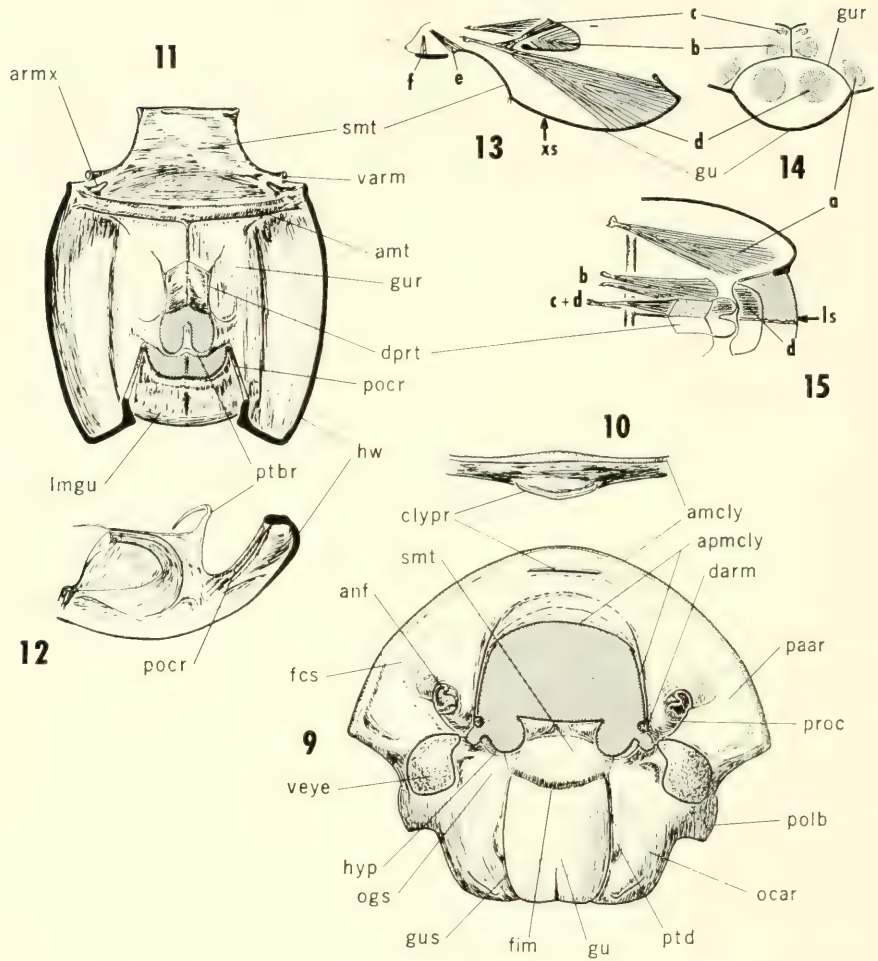
The cephalic process of both sexes is a hollow outgrowth of the head wall. Because the fronto-clypeal sulcus is incomplete medially, it is impossible to know the exact morphological identity of the area of the head bearing the cephalic process. That is, it cannot be known with reasonable certainty where the clypeus ends and the parietals begin in this area.

In some phanaeines, including *vindex,* there appears dorsally and laterally on the caudal portion of the head capsule a strong, bowed setose ridge (Figs. 4, 8, ocr). It marks no corresponding internal ridge and probably represents a secondary thickening rather than a true occipital sulcus. Primarily because of its position, I call it the *occipital ridge* and the dorsal and lateral areas of the head wall between it and the postoccipital suture the *occipital area* (ocar). Similar occipital ridges occur in some other dung beetles; Matthews (1961) first referred to them as transverse occipital carinae in *Copris.* In American Canthonina the occipital ridge provides important characters at the generic level (Halffter, *in litt.*). The morphological implications of "occipital" designations are justifiable since the occipital area is presumably, at least in part, composed of true occiput. Dorsally the occipital area is nearly suppressed because of the close approximation of the occipital ridge and postoccipital suture; laterally it is expanded, flattened and slightly depressed.

The *postoccipital suture* (Fig. 8, pocs) is visible only dorsally as a fine line closely following the posterior margin of the head. Laterally it is obliterated where it apparently coincides with the lateral margins of the occipital foramen. Thus, a very narrow *postocciput* appears only dorsally. Dorsally the postoccipital suture marks a deep, plate-like invagination continuous laterally with much narrower, rim-like inflections of the posterior margin of the head wall. This continuous inflection is the *postoccipital ridge* (Fig. 8, pocr). The ventral extremities of the postoccipital ridge are continuous with the tentorial structure described below.

The *occipital foramen* is a dorso-ventrally elongate opening in the posterior head wall (Fig. 8, ocfor). Its ventro-lateral angles are rounded, and in them articulate the apices of the cervical sclerites.

The ventral surface of the anterior portion of the head wall formed by the clypeus and paraocular areas of the parietals has been mentioned above. The *antennal sockets* are located in depressions of the paraocular areas marked posteriorly by the *preocular carinae* (Fig. 9, proc). A laterally-directed, conical *antennifer* (anf) projects from the mesal margin of each antennal socket. Antero-mesally the ventral portion of each eye closely approaches the base of the mandible, from which it is separated by a narrow, vertical portion of the head wall, the *oculo-malar space* (= pleurostoma?). In some dung beetles (e.g., *Scarabaeus*) this area is separated by a weak



FIGS. 9-15. *Phanaeus vindex*, male. **9**, head, ventral view; **10**, median portion of anterior margin of clypeus, frontal view; **11**, ventral head wall, internal view; **12**, dorsal process of tentorium, lateral view; **13-15**, maxillary muscles originating on tentorium, diagrammatic: **13**, longitudinal (parasagittal) section (xs=plane of cross section in Fig. 14); **14**, cross section; **15**, dorsal view (cf., Fig. 11; ls=plane of longitudinal section in Fig. 13).

suture extending from near the dorsal articulation of the mandible (i.e., the supposed position of the anterior tentorial pit) to the eye. This suture, which is obscured in phanaeines, is possibly part of a subgenal (pleurostomal) suture.

Ventrally the posterior portion of the head capsule of scarabaeids is strongly convex. Its most conspicuous element is the *gula* (Fig. 9, gu), a large, central, bulging sclerite. The gula is located between the ventral extensions of the postoccipital suture, which for convenience are referred to as

gular sutures (gus) (a cervical origin of the gula is assumed). The anterior external limit of the gula is approximated by a dense, transverse row of setae comprising the *labio-gular fimbria* (Fig. 9, fim). Removal of these setae from dung beetles reveals no suture, ridge or other line marking the junction between the gula and submentum; it reveals only a line of change in sculpture between the smooth gula and setigerously punctate submentum. In other Scarabaeidae (e.g., *Phyllophaga*), however, an entirely similar, presumably homologous row of setae occurs along a definite labio-gular suture. It appears reasonable, then, to consider the labio-gular fimbria of Scarabaeinae the definitive line of fusion of the gula and submentum. The posterior margin of the gula (Fig. 8, imgu) is strongly inflexed and consolidated with the ventral extremities of the postoccipital ridge. The submentum is fused laterally with the oculo-gular spaces and forms an integral part of the ventral head wall.

The remaining portion of the head capsule mesal and posterior to the ventral portions of the eyes can best be considered as three indistinct paired areas (Fig. 9). The first two are the ventral extensions of the occipital area (ocar) and postocular lobes (polb). The third is the *oculo-gular space* (ogs), that area between the margin of the eye and the lateral margins of the gula and submentum. Because of the lack of ventral extensions of the occipital sulcus, the morphological composition of the oculo-gular space is indeterminable; this space could be fused parts of the subgena or facial area (*sensu* DuPorte, 1960). If DuPorte is correct, the extent of the areas occupied by the ventral portions of the eyes of such scarabaeids as *Phyllophaga* indicates that the oculo-gular spaces are formed mostly by an invasion of the parietals onto the ventral surface of the head at the expense of the postgenae, which are greatly or completely replaced. This suggestion is further supported by the absence of an occipital ridge in many phanaeines and other dung beetles so that occipital and postgenal areas appear so consolidated with the parietals as to lose their identity.

The antero-mesal margin of each oculo-gular space bears a solidly fused, dorsally flexed sclerite adjacent to the antero-lateral angle of the submentum; this raised area is a *hypostoma* (Fig. 9, hyp). Dorsolaterally each hypostoma bears a small acetabulum, the *ventral articulation of the mandible* (Fig. 11, varm), which receives the mandibular condyle.

The *posterior tentorial pits* (Fig. 9, ptd) are represented by wide depressions in the ventral wall of the head at the sides of the gula. Internal examination of the gula, however, reveals a well developed tentorium supported laterally by invaginations along the entire lengths of the gular sutures rather than along the restricted areas indicated by the depressions. As DuPorte (1960) concludes for *Phyllophaga*, the gular sutures of dung beetles are probably best interpreted morphologically as elongations of the posterior

tentorial pits, and the gular ridges as expanded bases of the posterior tentorial arms. For descriptive clarity, however, use of the terms gular ridge and gular suture will be continued.

The *tentorium* of *vindex* conforms to the very uniform structure found in the Scarabaeinae studied. The invaginations of the gular sutures, the *gular ridges* (Figs. 11, 14, gur) fuse medially to form a thinly sclerotized roof over the gula.[3] A strong antero-dorsal flexion of the posterior portion of this roof has produced what resembles a dorsally projecting platform supported medially by a vertical, longitudinal lamella. This platform is the *dorsal process of the tentorium* (Fig. 12, dprt). Posteriorly it extends as a very delicate, E-shaped *posterior tentorial bridge* (ptbr). Extremely delicate filaments connect the antero-lateral angles of the dorsal process with the anterior tentorial arms; in Figures 5 and 11 only incomplete portions of these filaments are shown. Originating on the dorsal process of the tentorium of *vindex,* and presumably other dung beetles, are two paired muscles. One (Figs. 13-15, c) inserts *on the tendon* of a much larger muscle (d) originating posteriorly on the gula and inserting on the ventral posterior angle of the stipes; the other (b) divides apically into two sub-bundles, both of which insert on the cardo *mesal to* the maxillary articulation (Fig. 23). A third pair of maxillary muscles (a) originates posteriorly on the gular ridges and inserts on the articular process of the cardo *lateral to* the maxillary articulation. Muscles b, c and d are adductors of the maxillae; a is an abductor.

The *anterior margin of the tentorium* (Fig. 11, amt) is thickened and resembles a bar arching between the internal antero-lateral angles of the gula. Associated with the ends of this "bar" are two mesally-directed processes, the *maxillary articulations* (armx), on which articulate the cardines.

The *hypopharynx* forms with the prementum a compound structure treated below along with the labium.

APPENDAGES OF THE HEAD

As is characteristic of Scarabaeinae, the lamellate *antennae* are nine-segmented (Fig. 16-17). The posterior margin of the first segment, or *scape* (sp), bears a row of long setae, the *scapal fringe* (spfr), which reposes over the ventral surface of the eye. The second antennal segment is the *pedicel* (ped); the remaining seven segments comprise the *flagellum* (fla).

The last three antennal segments, the *lamellae,* together constitute the *antennal club* (Fig. 17). The form of the lamellae and antennal club is very characteristic of phanaeines and may be described as the *Phanaeus*-type. The basal lamella (seventh antennal segment) is scoop-shaped because of the concave distal surface which receives the smaller, similarly shaped second lamella. The terminal lamella (ninth segment) is received by the second; it

[3] In *Anomiopsoides,* a curious South American eucraniine, the gular ridges are not fused medially but are widely separated as in *Phyllophaga.*

is rounded and only slightly hollowed distally. Unlike the rest of the antenna, the lamellae are soft and fleshy except for the proximal, convex surface of the first, which is lightly sclerotized.

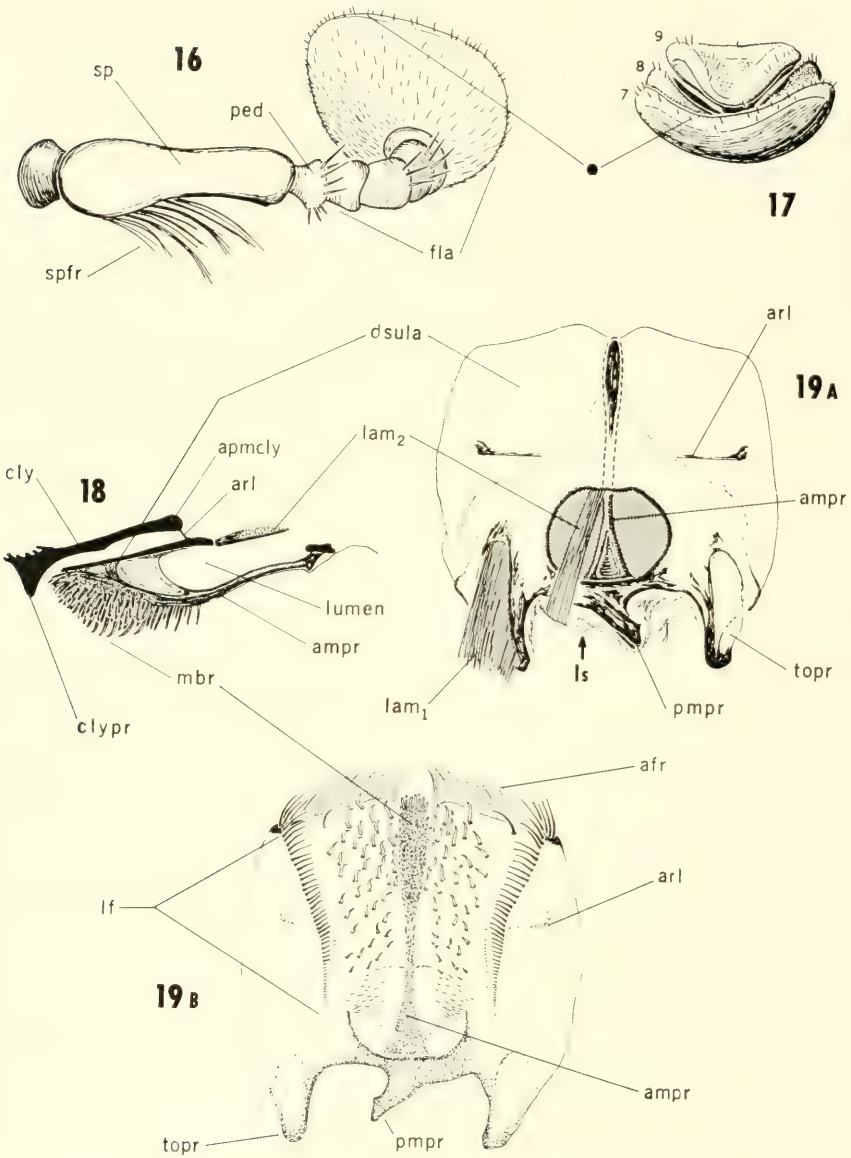
Although such modification of the antennal club is characteristic of phanaeines, it is not restricted to them. An instance of convergence is the *Phanaeus*-type antennal club of the South African genus *Sceliages*. The antennal club of the male of the Bornean *Onthophagus egregius* Arrow is similar to the *Phanaeus*-type, while that of the Palaearctic geotrupine genus *Lethrus* is modified in a similar, though distinct manner.

While the following account deals specifically with *P. vindex,* its mouthparts are illustrative of peculiar, though quite uniform structures characteristic of the whole subfamily. The mouthparts of adult Scarabaeinae (and some Aphodiinae) are quite unlike their usually more generalized counterparts in other beetles. As pointed out by Halffter and Matthews (1966) and others, they are highly modified for the manipulation of soft food, such as dung. The earliest discussion of adult scarabaeine mouthparts (those of *Dichotomius* [as *Copris*] *carolinus*) is that by Smith (1892), which deals primarily with the mandible. An excellent early study by Hardenberg (1907) compared the mouthparts of *D. carolinus* (as *Pinotus*) with those of other dung beetles, including *Phanaeus carnifex* (= *vindex,* not *sulcatus*), and with those of many other Scarabaeidae. Other general discussions include MacGillivray (1923; *Pinotus*), Mohr (1930; *Canthon, Bolboceros* and *Aphodius*), Madle (1934; *Aphodius*), Halffter (1961; *Canthon*) and Halffter and Matthews (1966; *Phanaeus*).

The mouthparts are here considered to include the *labrum* (= labrum-epipharynx of authors). Such consideration is supported partly by the morphological postulate that the labrum of insects is appendicular in origin but primarily by the curious morphology of the labrum of dung beetles, which suggests that it functions more as a mouthpart than a "preoral flap." The labrum ("labro-epifaringe") of *Canthon* is discussed at length by Halffter (1961).

Except for the suspensorium, the labrum is a dorso-ventrally flattened, squared flap lying in a horizontal plane on the lower surface of the head. Figure 18 shows diagrammatically its position relative to the head wall. It is joined by a narrow membrane (arl, representing the labro-clypeal sulcus) to the apical margin of the clypeus. The median portion of this articular line is seen dorsally on the extracted labrum as a transverse sclerotic thickening (Fig. 19A, arl). Anterior to this line is the *dorsal surface of the labrum* (dsula),[4] which in other beetles is usually visible externally.

[4] Reference to position in discussion of mouthparts will be made in the definitive (prognathous) sense rather than the morphological (hypognathous) one. Hence, the morphological anterior surface of the labrum is called the dorsal surface, etc.



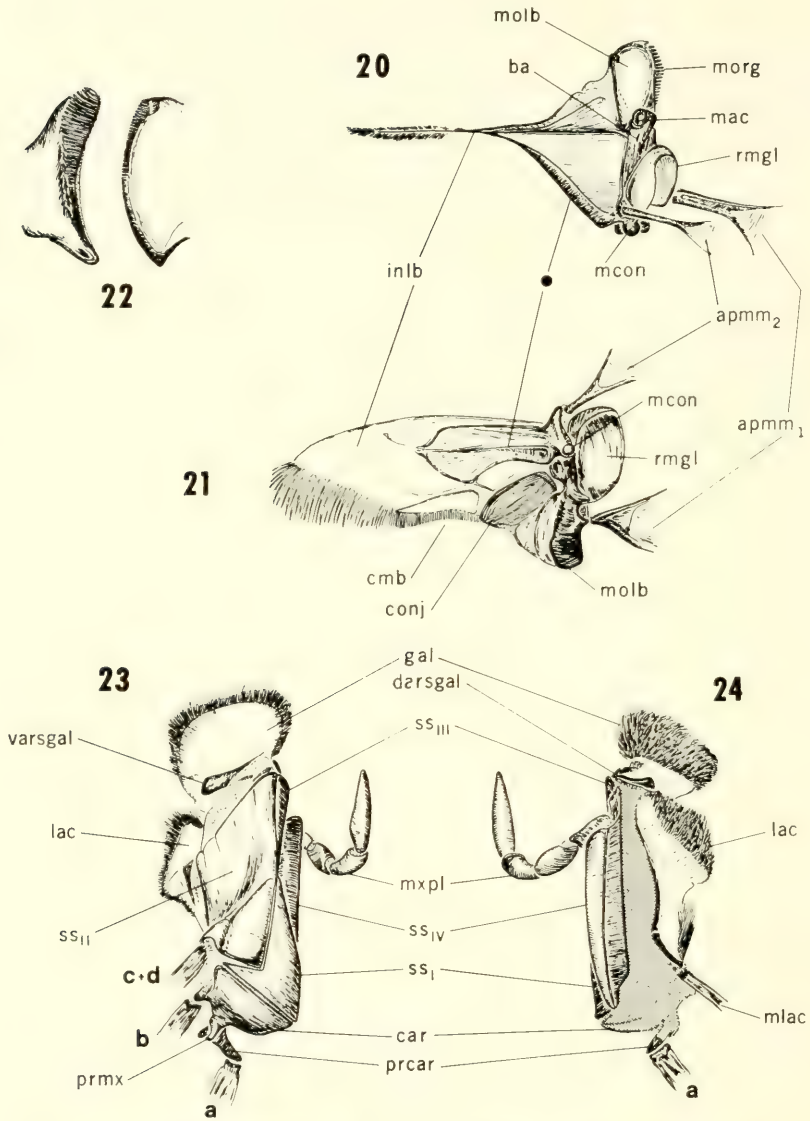
FIGS. 16-19. *Phanaeus vindex,* male. **16,** left antenna, ventral view (last two segments not visible); **17,** same, side view of antennal club (7, 8 and 9 indicate segment number); **18,** labrum and portion of clypeus, longitudinal (parasagittal) section; **19A,** extracted labrum, dorsal view (muscles shown unilaterally; ls=plane of longitudinal section in Fig. 18); **19B,** same, ventral (oral) surface.

Posteriorly the labrum extends internally as a strongly sclerotized supporting structure, the *labral suspensorium* (Figs. 18-19A). Posterior extensions of the labral suspensorium form three processes, two lateral *tormal processes of the labral suspensorium* (topr) and a *postero-median process* (pmpr) which from above is strongly bent to the right. Extending to the apex of the labrum is the *antero-median process* (ampr, = "vástago claviforme" of Halffter, 1952), a slender projection lying between the dorsal and ventral labral walls and adherent to the latter (Fig. 18). Apically the antero-median process expands dorso-ventrally, joining the upper and lower labral walls; ventrally this expansion bears the large setae of the *median brush* (mbr). Inserting laterally on each tormal process is a large muscle (lam_1) originating on the dorsal head wall directly behind the cephalic process; these muscles presumably depress the apex of the labrum. The insertion of these muscles suggests that the tormal processes represent the tormae (*sensu* Snodgrass, 1935) of other insects; indeed, the labral suspensorium might be the highly modified product of fusion of the tormae. A much shorter, second pair of muscles (lam_2) extends between the anterior edge of a large round hole in the suspensorium and the membrane between the tormal and postero-median processes; they presumably pull this membrane forward. Band-like thickenings of the membrane posterior to the tormal processes connect the labral suspensorium laterally to the bases of the mandibles, maintaining a close appression of the labrum upon them.

The lumen between the labral suspensorium and the ventral wall of the labrum (Fig. 18, lumen) contains an extensive network of exocrine glandular material, the secretions of which may serve such ends as brood ball construction (as an adhesive) or brood ball protection (as an antibiotic preventing bacterial and fungal growth, etc.).

The *ventral surface of the labrum* (Fig. 19B) is membranous and bears several types of regularly distributed setae. The *median brush* (mbr) is a longitudinal clump of thick, closely set setae inserted in the antero-median process of the labral suspensorium. Lateral to the median brush are similar setae scattered in a thick mat of short, fine hair. Two lateral, apically divergent longitudinal rows of prostrate setae comprise the *lateral files* (lf). The space between the lateral files is the *median area of the labrum* ("zona central" of Halffter, 1961); those spaces outside them, the *lateral areas* ("zonas laterales"). The lateral areas are clothed by long, silky hairs similar to the longer ones along the apical margin comprising the *apical fringe* (afr).

The membrane extending posteriorly from the labral suspensorium (continuous with the ventral surface) covers the upper ends of the molae of the mandibles and extends farther backward to form the dorsal wall of the buccal cavity. The ventral surface of the labrum rests against the mandibles with its median brush between the flattened incisor lobes of the mandibles.



FIGS. **20-24.** *Phanaeus vindex,* male. **20,** left mandible, lateral view; **21,** same, ventral view; **22,** molar lobes of mandibles, caudal view; **23,** left maxilla, ventral view; **24,** same, dorsal view.

Of the mouthparts, the *mandibles* are perhaps the most curiously modified (Figs. 20-21). Smith (1892), followed by Hardenberg (1907) and others, recognized several more-or-less distinct parts which he considered homologs of maxillary sclerites. For *descriptive* purposes, it is convenient to recognize

four mandibular parts: the basalis (Smith), incisor lobe, conjunctivus (Smith) and molar lobe.

The *basalis,* or basal piece, is heavily sclerotized and bears the articulations and muscle insertions of the mandible (Fig. 20, ba). The *mandibular acetabulum* (mac, dorsal articulation) fits over the condyle on the posterolateral extremity of the apical margin of the clypeus. The *mandibular condyle* (Figs. 20-21, mcon; ventral articulation) fits into the acetabulum in the dorso-lateral angle of the hypostoma. Directly lateral to the mandibular condyle is a small swelling on which is inserted the fan-shaped apodeme ($apmm_2$) of the abductor muscle of the mandible; the larger apodeme of the adductor muscle ($apmm_1$) is inserted ventro-mesally on a swelling adjacent to the molar lobe. Both of these muscles originate on the postero-ventral head wall.

The *receptacle of the mandibular glands* (Figs. 20-21, rmgl) is thin-walled and cup-shaped; it is attached rather loosely to the posterior surface of the basalis. The receptacle contains a large mass of exocrine glandular tissue similar to that in the lumen of the labrum. Inserted medially on the receptacle is a large muscle (not shown in Figs. 20-21) with no conspicious apodeme which originates beside the adductor and abductor muscles on the head wall. Since its insertion is on a line between the dorsal and ventral mandibular articulations, it presumably does not function, at least efficiently, in gross mandibular movements. Rather, it likely moves the receptacle, perhaps to force discharge of the products of the mandibular glands.

The *molar lobes* (Figs. 20-21, molb) are dorso-ventrally elongate, mesal lobes of the basalis. Their transversely ridged mesal surfaces are asymmetrical (Fig. 22), the left concave and the right convex. Miller (1961) found each molar lobe to consist of a series of juxtaposed microscopic processes ("tritors") capable of extreme trituration of food particles. Dorsally the ridging of both molar lobes becomes very coarse and projects beyond the posterior margin, which appears serrate (Fig. 20, morg). *In situ* the molar lobes fit against the vertical posterior wall of the hypopharynx, which forms the anterior portion of the deeply concave floor of the buccal cavity. Only the dorsal ends of the molar lobes project above the posterior hypopharyngeal wall. Presumably, food entering the buccal cavity is first masticated by the coarser dorsal ridging and then more finely ground by the microscopic ridging after entering.

The basalis extends anteriorly as a dorso-ventrally flattened lobe thought to function as a food scraper and to correspond to the incisor lobe of the more generalized chewing mandible. Laterally this *incisor lobe of the mandible* (inlb) is strongly sclerotized, but it becomes decreasingly sclerotized and more translucent mesally. The apex of this lobe is repeatedly narrowly incised mesally and bears many long superficial setae (not shown

in Fig. 21). A double row of much shorter, closely-set setae comprising the *comb of the incisor lobe* (cmb; see Miller, 1961) occurs along the mesal margin of a weakly sclerotized, triangular area. This fringed area is referred to by Smith and several later authors as the "prostheca."

The *conjunctivus* (Smith) is a convex, soft and flexible "sclerite" on the ventral surface of the mandible between the comb of the incisor lobe and molar lobe (Fig. 21, conj). It appears longitudinally ridged, but as Halffter (1961) has pointed out, each "ridge" consists of a row of thick adherent setae. *In situ* the conjunctivus fits over the thick, lateral margin of the posterior hypopharyngeal wall lateral to the molar lobe, possibly functioning as a seal or strainer preventing circumvention of the coarsely ridged dorsal ends of the molar lobes by large food particles. Miller (1961) believes the conjunctivus ("flexible area of the mandible") cushions the grinding movements of the molar lobes and, possibly, permits independent molar movements "while the mandibles are in the closed position."

The *maxillae* articulate in a plane parallel to that of the mandibles. As seen ventrally (Fig. 23), they are well sclerotized appendages not markedly different from a generalized type, as are the labrum and mandibles. Each *cardo* (car) is rounded basally, and projecting mesally from its basal margin is the elongate *articular process of the cardo* (prcar). This process bears a forked lobe (prmx) which articulates with the maxillary articulation (Fig. 11, armx).

The *stipes* constitutes the bulk of the body of the maxilla. It is quadripartite, each division being separated from the others by membranous sulci (i.e., the parts can be disjoined quite easily). What are here considered three distal sclerites of the stipes have been considered two subdivisions of the galea and a palpifer in other studies of scarabaeine morphology (e.g., Mohr, 1930). The primary basis for the present interpretation is the intrinsic musculature of the maxilla, pertinent aspects of which will be brought out below. Although appropriate names for the parts of the stipes could be devised using descriptive prefixes, I have used numerical designations to avoid confusion with other maxillary terminology.

The basal sclerite of the stipes, *stipital sclerite I* (Fig. 23, ss_I; = stipes of authors) articulates with the cardo. On its internal surface originates a muscle inserted on the ventral articular sclerite of the galea (varsgal). *Stipital sclerite II* (ss_{II}; = subgalea of authors) is a large, rectangular piece. Distally it bears the galea, laterally the lacinia; its ventral surface bears a wide oblique ridge, mesal to which the surface is strongly concave. The concave area fits upon the apex of the labium and is hidden when the maxillae are closed. *Stipital sclerite III* (ss_{III}; = proxagalea of authors) is an elongate narrow piece interposed between the apices of sclerites II and IV. *Stipital sclerite IV* (ss_{IV}; = palpifer of authors) is also elongate and forms the lat-

eral portion of the maxilla. Only sclerite IV is well developed dorsally (Fig. 24). Originating on its base are two muscles, one inserting on the basal segment of the maxillary palpus, the other on the dorsal articular sclerite of the galea (darsgal).

The lobate *galea* (gal; = distagalea of authors) is articulated with the stipes by two transverse sclerotized bands, the *articular sclerites of the galea*. Both sclerites are free, one in the dorsal, the other in the ventral membrane of the base of the galea. Except for the articular sclerites, the galea is a thick, membranous lobe which is dorso-ventrally flattened and flexed ventrally over the apex of the labium. Dorsally it bears a dense pad of short, erect setae (Fig. 24).

The *lacinia* (lac) is an apically widened and truncate, flattened lobe. Since it is united laterally with stipital sclerite II and not intrinsically musculated, it is presumably not moved independently. Dorsally can be seen a sclerotized strip which basally bears a dense tuft of rather long setae. The apex of the lacinia bears a dorsal, densely setose pad like that on the adjacent surface of the galea.

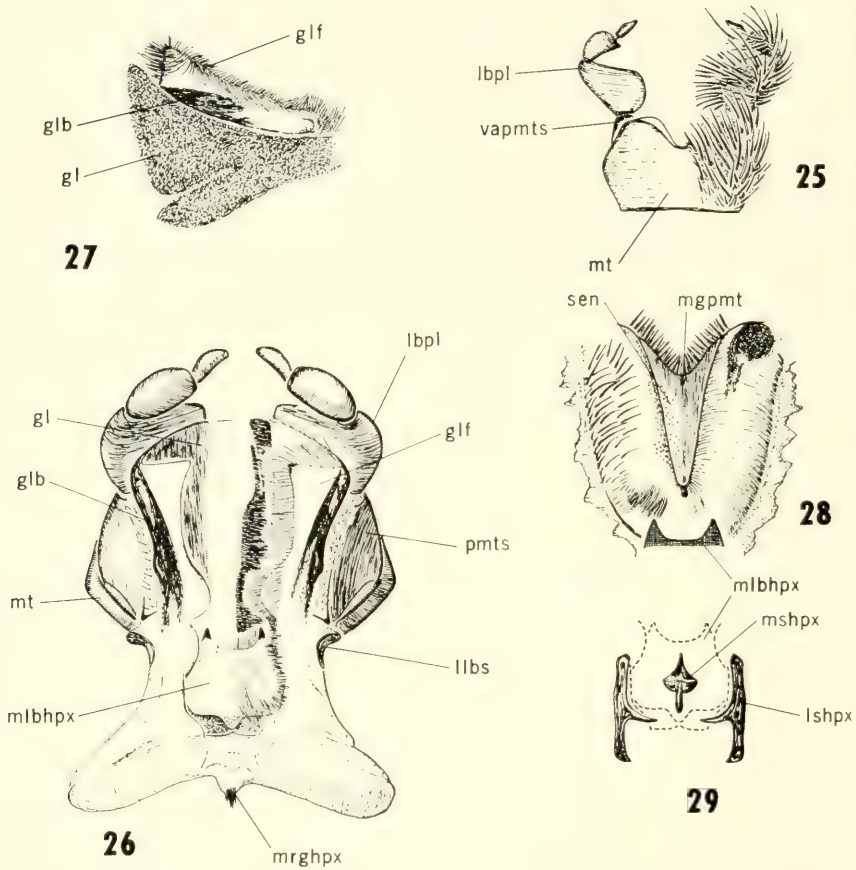
The *maxillary palpus* (mxpl) articulates in a large socket in the apex of stipital sclerite IV. It is composed of four cylindrical segments which are successively longer distally. The apex of the distal segment bears a small, supposedly sensory, membranous spot.

The cardo and stipital sclerites I and IV bear numerous long, stiff setae (not shown in Figs. 23-24). The remainder of the appendage, including the palpus, is either bare or with small, inconspicuous setae.

The four extrinsic muscles of the maxilla insert on conspicuous apodemes. Those three originating on the tentorium (and gula) have been described above. The letters designating apodemes in Figures 23 and 24 correspond to those designating muscles in Figures 13-15. The fourth (Fig. 24, mlac) originates on the head wall and inserts on the base of the lacinia.

As is generally true of beetles (Dorsey, 1943), the labial musculature of scarabaeines is considerably reduced and modified, making interpretation of the labium difficult by standard morphological criteria. Extrinsic muscles are absent and intrinsic ones are reduced in number. Likewise, the gross structure of the labium is curiously modified and difficult to compare with the generalized plan.

The *submentum* is generally identified as that postlabial sclerite on which originate the median muscles of the labium (Snodgrass, 1935; = submentopremental muscles of Matsuda, 1965). This pair of muscles is either absent or considerably modified functionally in dung beetles. My designation of the submentum (smt) in Figure 9 and elsewhere is based primarily upon its position relative to the posterior tentorial pits (gular sutures) and its presumed correspondence with similar, definitely premental plates in other



FIGS. 25-29. *Phanaeus vindex*, male. **25,** mentum and prementum, ventral view (setae shown unilaterally); **26,** prementum-hypopharynx, oral surface (setae shown unilaterally; floor of buccal cavity not shown, cf., Fig. 30); **27,** right glossa, mesal surface; **28,** median groove of prementum (glossae torn away; only apex of median lobe of hypopharynx shown); **29,** hypopharyngeal sclerites, dorsal view.

beetles. Snodgrass (1935:294) called the corresponding sclerite in *Phyllophaga* (Melolonthinae) the mentum, the submentum being represented by an internal plate on which originate the median muscles of the labium. He did not suggest the possibility that this internal plate represents only a posterior apodemal inflection of the submentum, the remainder of the sclerite being the exposed area distal to the gula. Kadić (1902), followed by Hardenberg (1907) and Mohr (1930), referred to the present submentum as the posterior plate of the submentum, the present mentum being the anterior plate. As described above, the submentum forms a part of the ventral head wall; distally it projects freely between the bases of the maxillae.

The *mentum* (Fig. 25, mt) articulates with the straight distal margin of

the submentum. It is emarginate anteriorly and densely clothed with long, stiff setae. Its postero-lateral angles are inflexed mesally; on them articulate the ventral extremities of the hypopharyngeal suspensorium (Fig. 33).

The remaining labial structures are borne on the dorsal surface of the mentum and, except for the palpi, are hidden. The *prementum* is represented by a pair of *premental sclerites* (Fig. 30, pmts), the wedge-shaped ventral angles (vapmts) of which articulate with the antero-lateral angles of the mentum. In many dung beetles, including some phanaeines, the premental sclerites are membranous medially and only a C-shaped margin is sclerotized (Fig. 150).

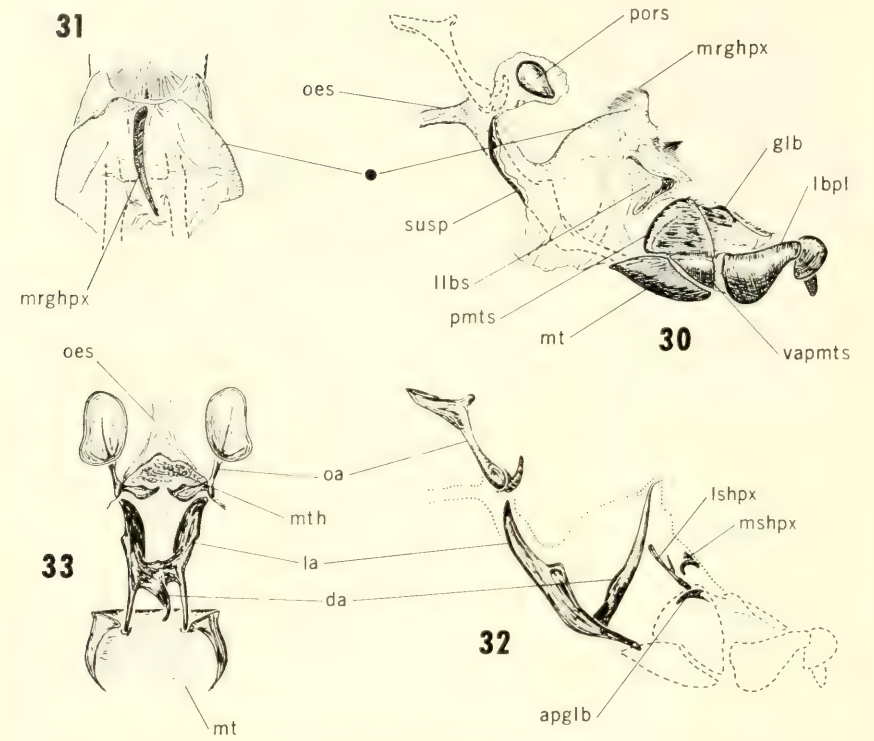
The three-segmented *labial palpi* (Fig. 25, lbpl) articulate on the ventral angles of the premental sclerites (Figs. 25, 30). The two proximal segments bear many long, stiff setae, while the distal segment bears a single, very small seta on the outer surface. As does the distal segment of the maxillary palpus, the distal segment of the labial palpus bears a small, presumably sensory, membranous apical spot. On the basal segment of each is inserted a single muscle originating on the posterior margin of the adjacent premental sclerite.

Projecting anteriorly from between the premental sclerites are two elongate, membranous lobes, the *glossae* (Fig. 26, gl). The use of the term glossa, however, is loose and not meant to imply either that paraglossae are present or that they have presumably been lost. The glossal structure of all dung beetles and other scarabs examined is problematic.

In all dung beetles examined, except *Anomiopsoides,* the mesal surfaces of the glossae are covered by a thick mat of short setae (Fig. 27) like that on the galeae and laciniae. Projecting mesally from the lateral margin of each glossa is the *glossal flap* (Figs. 26-27, glf), a translucent membranous flap fringed with long hairs. Seen mesally (Fig. 27), the glossae of phanaeines and some other dung beetles are apically bilobed. The slit separating these lobes is usually obscured by setae. One could assume that this slit is an incomplete division (latarima of MacGillivray, 1923) between the glossa and paraglossa, which are fused basally. However, consideration of the glossae of such scarabaeines as *Heliocopris,* which are trilobed, and of *Catharsius,* which are not notched, considerably weakens such an assumption.

The glossae are supported laterally by the *glossal bars* (Figs. 26, glb). Posteriorly these bars project internally (Fig. 32, apglb) and are closely connected but not fused with the antero-dorsal angles of the *lateral labial sclerites* (Figs. 26, 30, llbs).[5] Inserting on the connection of each of these two pieces is

[5] In *Heliocopris* the position of the lateral labial sclerites is occupied by a heavily sclerotized posterior extension of the glossal bar. This condition suggests that where lateral labial sclerites occur, they represent disjunct portions of the glossal bars. The strength of this suggestion, however, rests on a knowledge of the condition of the glossal bar in a wider variety of scarabaeines than that used for this study.



FIGS. **30-33.** *Phanaeus vindex,* male. **30,** extracted labium-hypopharynx (without submentum), lateral view (broken outline refers to Fig. 32); **31,** posterior wall of hypopharynx; **32,** suspensorium of hypopharynx and oral arms, lateral view (broken outline refers to Fig. 30); **33,** same, dorsal view (hypopharynx and prementum removed).

a muscle originating medially on the anterior margin of the submentum (Fig. 13, e). Since each muscle diverges from its origin, I assume that, as a pair, they function primarily to spread the glossae. They could, however, be interpreted either as glossal muscles, whose origins have shifted from the presumably primitive prelabial position to the postlabium (submentum), or as the median muscles of the labium, which functionally have become abductors of the glossae rather than levators of the prementum.

In certain phanaeines, including *vindex* and some other dung beetles, the glossae come together at least basally (Fig. 26). In others, their bases are separated to varying degrees (Fig. 149). If the glossae are spread apart, the *median groove of the prementum* (Fig. 28) is exposed. The raised sides of this groove bear long, mesally-directed setae. Its floor is weakly sclerotized and bears dark, generally scattered sensory spots (sen) which, on internal examination, resemble sensilla coeloconia.

Posteriorly the glossae are continuous with the *hypopharynx,* and together

they form a large, quadrate lobe on the dorsal surface of the mentum (Fig. 30). The membranous *median lobe of the hypopharynx* (Figs. 26, 28, mlbhpx) is above the apex of the median groove of the prementum and slightly covered laterally by the bases of the glossae. In species with separated glossae, the median lobe is completely exposed (Fig. 149) and covered with fine hair. Directly beneath the dorsal surface of the hypopharynx are three *hypopharyngeal sclerites*. A Y-shaped *lateral hypopharyngeal sclerite* (Fig. 29, lshpx) is on each side of the *median sclerite* (mshpx). Figure 29 shows their positions relative to the median lobe. Inserted on a hook-shaped ventral process of the median sclerite is a single (unpaired) muscle originating medially on the mentum (Fig. 13, f).[6] It supposedly depresses the median lobe of the hypopharynx. The vertical posterior wall of the hypopharynx is concave on each side of the *postero-median ridge of the hypopharynx* (Fig. 31, mrghpx). This ridge is bowed to the left to fit between the asymmetrical molar lobes of the mandibles, which fit against the hypopharynx.

Associated with the hypopharynx is a system of sclerotized bars comprising the *suspensorium of the hypopharynx* (Figs. 32-33). This supporting structure is well developed in dung beetles and consists of two *lateral arms* (la; = suspensoria of Snodgrass, 1935) joined by a thicker, transverse bar. The lateral arms also support the membranous floor of the buccal cavity; their ventral ends articulate with the mentum. Extending dorsally from the transverse bar is the *dorsal arm of the suspensorium* (da). It projects freely through the body of the hypopharynx to beneath the dorsal extremity of the postero-median ridge (Fig. 32) and supposedly prevents collapse of the otherwise soft, membranous hypopharynx.

The *oral arms* (Figs. 32-33, oa) are connected end-to-end with the lateral arms by thickened membranes. Ventrally they are bent mesally beneath the *mouth* (Fig. 33, mth). The dorsal ends of the oral arms are greatly expanded muscle discs ("tendon caps") on which insert short, thick muscles originating on the dorsal head wall behind the cephalic process. Since the arms are linked with the lateral arms of the suspensorium, which in turn articulate with the mentum, their muscles presumably effect elevation of the mentum (and prementum). From a functional morphological point of view, such function of these muscles, which are generally retractors of the hypopharynx (Snodgrass, 1935), is logical since median muscles (elevators) of the prementum are apparently absent (see above).

The *paraoral sclerites* (Fig. 30, pors) are oval, sclerotized thickenings in the lateral walls of the buccal cavity. On each is inserted a muscle from the head wall which presumably dilates the cavity.

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[6] Dorsey (1943) describes a similar unpaired muscle ("median muscle of the labium") in *Popillia japonica* (Rutelinae), but he finds it in no other beetle examined (p. 32), including *Macrodactylus* (Melolonthinae).

THE CERVIX

The *cervix* is the membranous region extending from the margin of the occipital foramen to the inflexed anterior margin of the prothorax. It is fairly long and allows the head to be forcibly withdrawn beyond the prothorax, although the head is probably never protracted this far by the living beetle. The cervix allows free movement of the head, but movement is largely restricted to a vertical plane by the tight fit of the posterior portion of the head within the prothorax.

Located latero-ventrally in each side of the cervix is a single elongate *cervical sclerite* (Fig. 34). It articulates basally with the inflexed antero-lateral angle of the propleuron and apically with the rounded ventro-lateral angle of the occipital foramen. The setose external surface of the sclerite is concave; the internal surface is ridged for muscle attachment. Upon retraction of the head, the apices of the sclerites fold dorso-mesally against the recessed anterior prothoracic margin. Situated dorsally in the cervix near the posterior head margin is a pair of lightly sclerotized, setose pads. Halffter (1961) has referred to similar pads in *Canthon* as anterior cervical sclerites. In view of their dorsal position and the double articulation of the cervical sclerite, it seems doubtful that they represent anything more than thickenings of the cervical membrane.

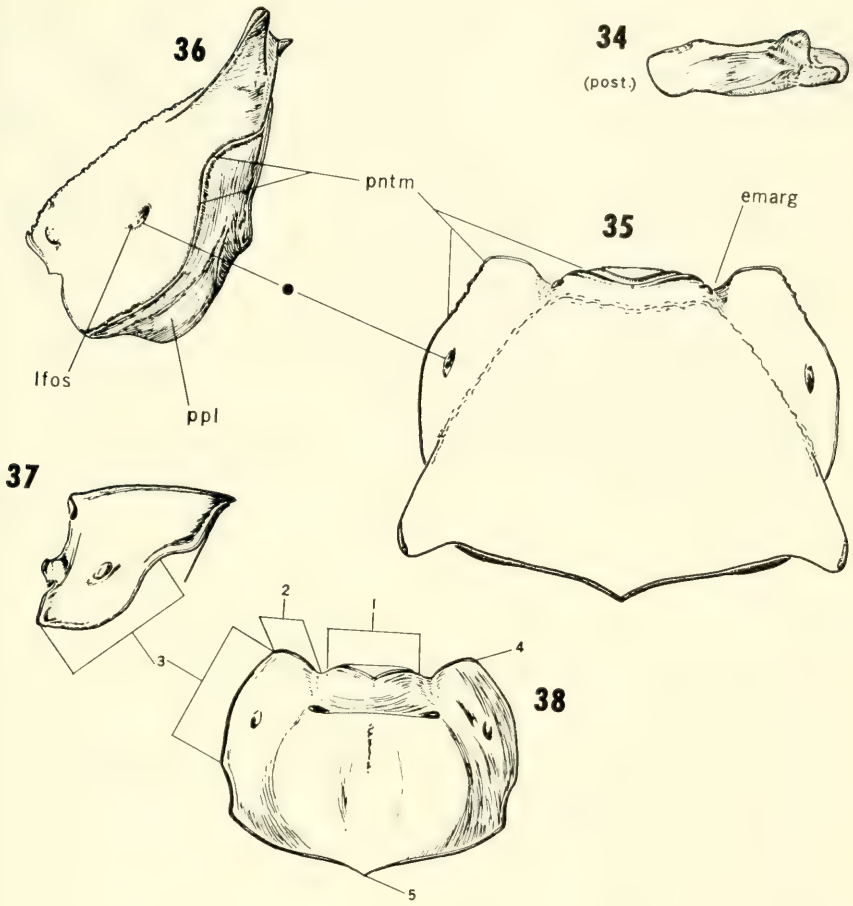
THE THORAX

THE PROTHORAX

The large, box-like prothorax accommodates the strongly developed muscles effecting movement of the head and front legs, the principal digging organs. Its anterior margin (to which is connected the cervical membrane) is recessed. The sclerites contributing to the anterior margin are all strongly inflexed and shaped to receive the posterior part of the head.

Like the head, the *pronotum* of dung beetles and other "horned" scarabaeids often bear outgrowths (protuberances, ridges, etc.) producing forms characteristic of species. As are those of the head, such outgrowths are allometric and usually only the males bear well developed "armature." The pronotum of a well developed male of *vindex* is shown in Figures 35 and 36; that of the female in Figures 37 and 38. In less well developed ("minor") males, its angulate appearance is less well marked. Sexual differences as exhibited by the prothorax are pronotal; the propleurae and sterna of both sexes are respectively alike.

In phanaeines, a distinct *postero-median angle of the pronotum* (Fig. 38, 5) fits between the bases of the elytra and covers the mesonotum. In some species this angle bears two distinct impressions, the *posterior pronotal fossae* (Fig. 194, pfos). On each side of the pronotum of all dung beetles (except some Canthonina—Halffter *in litt.*) there is a shallow, usually smooth depression, or *lateral pronotal fossa* (Fig. 36, lfos), marking an internal tubercle



FIGS. **34-38.** *Phanaeus vindex*. **34,** right cervical sclerite, lateral view (post. indicates posterior end); **35,** prothorax of well developed male, dorsal view; **36,** same, lateral view; **37,** prothorax of female, lateral view; **38,** same, dorsal view (1-5, sections and angles of circumnotal ridge: 1—anterior portion, 2—antero-lateral portion, 3—lateral portion, 4—antero-lateral angle, 5—postero-median angle).

on which articulates the base of the procoxa (Fig. 40, acx). In both sexes of *vindex* the pronotum is very strongly rugose (Fig. 165).

The *circumnotal ridge* (Figs. 35-36, pntm) is a sharp ridge separating the definitive pronotum from the rest of the prothorax. For descriptive convenience, various sections and angles of this ridge are defined in Figure 38. The sinuous lateral portion (3) is characteristic of the majority of phanaeines. The transverse anterior portion (1) is widened and in most dung beetles is continuous with the antero-lateral portions (2). In *Phanaeus,* however, the anterior portion is interrupted on each side by a distinct, rounded emargina-

tion (Fig. 35, emarg) into which fits the prominent postocular lobe of the parietals. The morphological significance of the circumnotal ridge is unclear. It is present in all scarabaeids and separates a dorsal area of the prothorax (pronotum) which differs usually in integumental sculpturing and often in color from the ventral areas (pleura and sternum).[7]

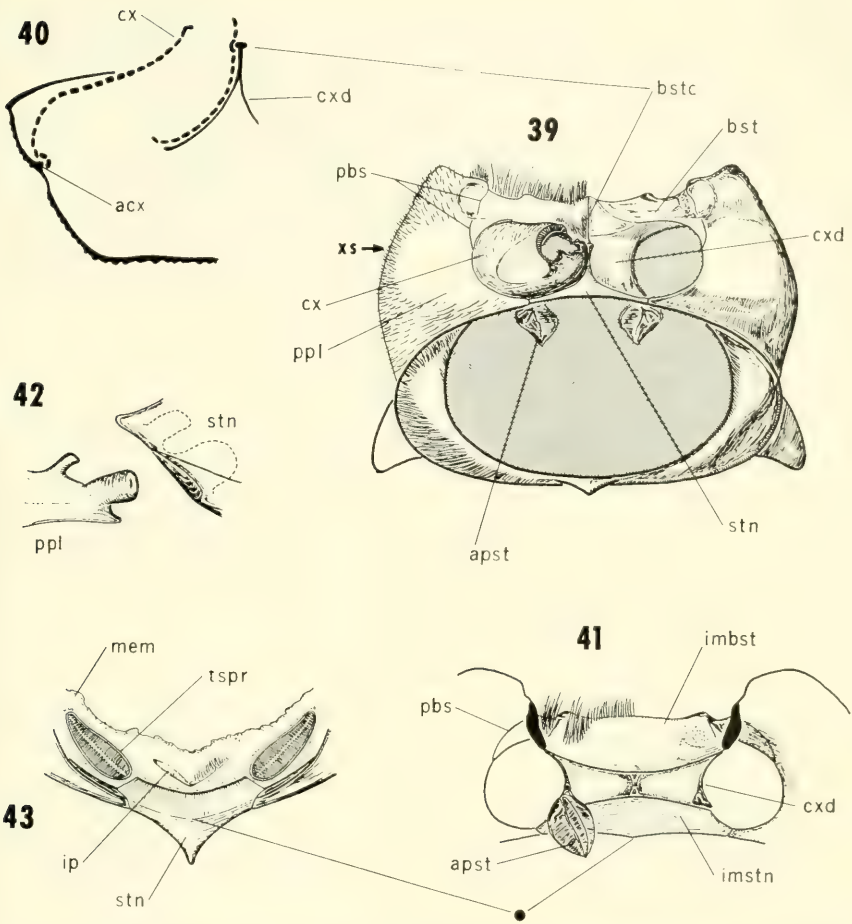
A very large, round opening in the flattened posterior wall of the prothorax (Fig. 39) fits over a protruding rim formed by parts of the mesothorax. The lateral portions of this wall are widest and shaped so as to fit snugly against the opposing areas of the mesopleura.

Except postero-laterally, the *propleura* (Figs. 36, 39, ppl) are ventral areas of the prothorax. Each propleuron is setigerously punctured except for a smooth, raised area lateral to the procoxal cavity. As seen ventrally (Fig. 39), their mesal margins are the curved lateral margins of the coxal cavities. A postcoxal extension (postcoxale) of each pleuron is joined with the lateral angle of the sternellum (stn) by a double pin-and-socket mechanism shown in Figure 42. Each propleuron is fused anteriorly with the lateral margin of the basisternum along the *pleurobasisternal suture* (Fig. 39, pbs). The propleura of a few phanaeines (*Dendropaemon*) and some other dung beetles (e.g., *Copris* and *Eurysternus*) are each divided by a *transverse propleural carina* (Figs. 179-180, arrows). This carina extends laterally from the coxa, separating a "proepisternum" and "proepimeron." Since there is never an internal ridge corresponding to it, the carina is probably best interpreted as a secondary integumental feature rather than as a primary division between pleurites. In many dung beetles, including some phanaeines, the anterior portion of each propleuron ("proepisternum") is strongly concave or otherwise set off from the "proepimeron."

Coincident with the expansion of the prothoracic box, the procoxae have become transversely oriented, cylindrical structures whose apices nearly touch each other mesally. The propleura have expanded ventro-mesally and cover the bases of the coxae, which articulate internally with the lateral pronotal walls. Their transverse orientation has affected the structure of the *prosternum*, a portion of which is depressed and hidden by the apices of the coxae. Thus, only a portion of the prosternum is visible with the coxae *in situ*.

The exposed portion of the *basisternum* (Fig. 39, bst) is anterior to the front coxae and between the pleurobasisternal sutures. Its anterior margin (Fig. 41, imbst) is reflexed posteriorly and shaped to receive the gula and

[7] Butt (1944) has not differentiated notal and pleural areas in the prothorax of *Amphimallon* (Melolonthinae), but, rather, considers all prothoracic areas except the sternum as pronotal (p. 11). There seems to be some validity to his designation (which could be applied equally well to dung beetles) if, for example, one negates the supposedly "homodynamous" evolution of all thoracic segments, particularly their pleura. Nevertheless, mainly because of its established use in beetle taxonomy, I choose to maintain at least descriptive distinction between pronotum and propleura.



FIGS. 39-43. *Phanaeus vindex,* male. **39,** prothorax, ventral view (right coxa in place; setation shown on beetle's right only; xs=plane of cross section in Fig. 40); **40,** same, cross section through right side; **41,** prosternum, internal view (right prosternal apophysis removed; setation shown on left side only); **42,** interlocking mechanism of sternellum and propleuron, right side (broken outline indicates cavities in sternellum receiving pleural lobes); **43,** sternellum and adjacent parts, posterior view (mem=intersegmental membrane).

adjacent occipital areas of the head. The *basisternal crest* (Figs. 39-40, bstc) is a median, longitudinal ridge extending posteriorly between the apices of the coxae to the anterior angle of the sternellum. A tuberculate swelling on each side of this crest articulates in a groove (Fig. 60, groove) in the apex of the coxa. These tubercles are secondary sternal articulations of the front coxae, primary articulations (with the lateral margins of the sternum) being hidden by the extensive overlap of the coxae by the pleura. The exposed portion of the *sternellum* (Fig. 39, stn) is triangular, the apex directed be-

tween the coxae and fused with the basisternal crest. Its posterior margin (Figs. 41, 43, imstn) is reflexed anteriorly and forms a shelf fitting over the mesosternum.

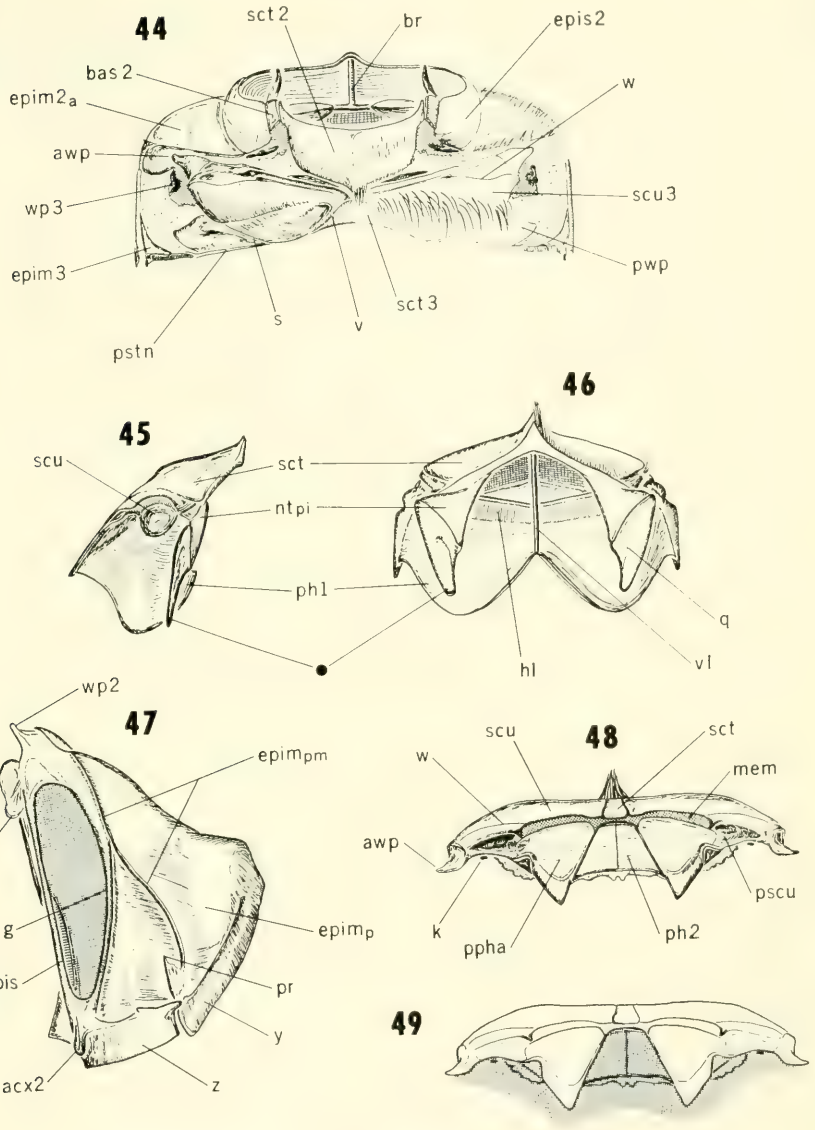
Removal of the front coxae reveals the hidden portion of the prosternum, a smooth trough on each side of the basisternal crest in which rotates the apex of the coxa (Fig. 39, cxd). Projecting from the lateral margin of each trough is a *prosternal apophysis,* a petiolate structure composed of three vertical lamellae (Figs. 39, 41, apst). To the apophyses are attached muscles from the posterior head margin, from the procoxae and from phragma I. The positions of these apophyses indicate that the depressed portions of the prosternum are composed of roughly equal parts of basisternum and sternellum, although there is no visible line between the two.

Located latero-ventrally in the pro-mesothoracic intersegmental membrane on each side of the sternellum is a very large, spindle-shaped *thoracic spiracle* (Fig. 43, tspr). There is only one pair of thoracic spiracles. Between them is a V-shaped, setose *interspiracular pad* (ip), which, along with the spiracles, is probably never exposed during normal activity. Ritcher (1969a, b) discusses the spiracles of *vindex* and other scarabaeids.

THE PTEROTHORAX

Restriction of flight power to the hind wings is correlated with a proportionately large metathorax, which contributes the bulk of the volume of the pterothoracic box. Except for the mesepimera, the mesothorax forms a constricted rim over which fits the prothorax. Except in *Anomiopsoides,* which lacks hind wings, the pterothoracic structures of all scarabaeines examined are quite similar.

As seen dorsally, *in situ* (Fig. 44), the mesonotum appears as a single, pentagonal sclerite between the articular processes of the elytra. Much of it, however, is inflected and hidden by the close approximation of adjacent sclerites. Figures 45 and 46 show these external aspects of the mesonotum. Interpretation and naming of the mesonotal areas are difficult. A "V-suture" (Snodgrass, 1935 and elsewhere) separating scutum and scutellum is either lacking or unrecognizable. Furthermore, internal ridges, while well developed, are probably not indicative of basic notal divisions. Primarily because standard taxonomic terminology is based on it, it seems best to follow Snodgrass' interpretation (1909 and elsewhere) of the pterothoracic nota. Accordingly, the dorsally exposed, pentagonal mesonotal area is the *scutellum* (Fig. 44-46, sct2). In a few dung beetles (e.g., *Eurysternus, Megathopa* and *Onitis*) and in many other scarabaeids, a posterior, triangular portion of the mesoscutellum (usually very small in dung beetles) is permanently exposed between the bases of the elytra and not covered by the pronotum. The *mesoscutum* (Fig. 45, scu) is divided by the scutellum and represented on



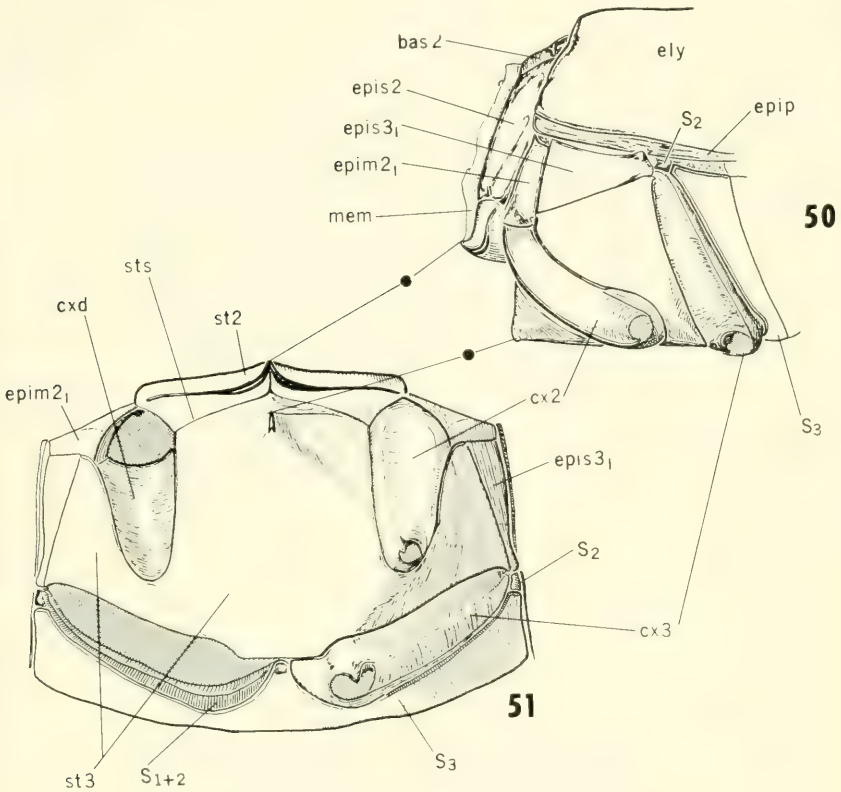
FIGS. 44-49. *Phanaeus vindex,* male. **44,** pterothorax, dorsal view (elytra and hind wings removed; setation shown on right only); **45,** extracted mesonotum, lateral view; **46,** same, posterior view; **47,** extracted mesopleuron, internal view; **48,** extracted metanotum, anterior view; **49,** same (stippling indicates internal structures).

each side of it by a rounded inflection of the notum on which articulates the first elytral axillary sclerite. A longitudinal, mid-dorsal line on the scutellum marks a deep, vertical plate (Fig. 46, vl) fused anteriorly to phragma 1. This plate intersects a narrower, horizontal plate (hl) extending between the scutal areas and also fused to phragma 1.

The *posterior inflection of the mesonotum* (Figs. 45-46, nt_{pi}) is strongly downflexed and widely emarginate. The origin of this margin is not clear; it may be scutellar, a remnant of the mesopostnotum, or of another origin. Functionally, however, it appears to be a mechanism allowing firm contact of the pteronota. The rounded (lower) margin of the inflection is joined *very* closely to the margin of phragma 2 by the intersegmental membrane. Articulating at each side of the inflection is a vertical, triangular plate corresponding to that which Snodgrass (1909) refers to as *sclerite q* (Fig. 46, q) in other beetles. Snodgrass suggests that sclerites q might represent the remains of a mesopostnotum. Inserted on it is a large muscle originating on phragma 1.

At each side of the mesonotum, in front of the articular processes of the elytra, is a rectangular *mesobasalare* (Figs. 44, 50, 52, bas2). Each is produced subintegumentally as an acute apodeme (Fig. 52, abas2) on which originate two muscles, one inserting on the mesocoxal margin, the other on the base of the trochanter.

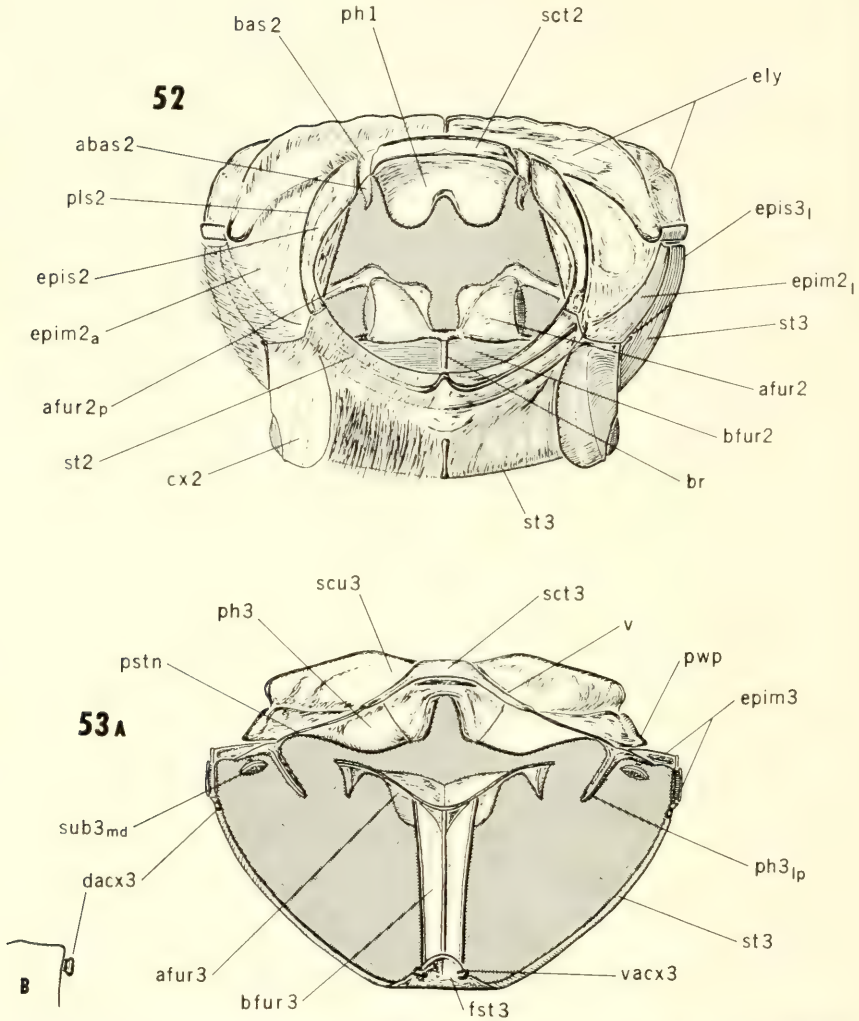
The metanotum more nearly conserves typical pterothoracic structure than does the mesonotum. It is irregularly convex and much wider than the mesonotum. Figure 44 shows its surface areas and sutures. Like the mesoscutum, the *metascutum* (scu3) is divided medially by the *metascutellum* (sct3), from which it is separated by the V-suture (v). An oblique suture (s) on each side of the scutum sets off a triangular, postero-lateral scutal area, the lateral angle of which is the *posterior metanotal wing process* (pwp). Originating on each side of the metascutum are two large muscles, both of which insert on the anterior margin of the metacoxa. The *prescutum* (Fig. 48, pscu) forms an anterior surface of the metanotum hidden *in situ* by the mesothorax and separated from the scutum on each side by a weak, transverse w-suture (Figs. 44, 48, w). Lateral projections from the prescutum are the *anterior metanotal wing processes* (awp). *The paraphragmal areas of the prescutum* (Fig. 48, ppha) are fused with the lateral margins of phragma 2 along the line of attachment of the intersegmental membrane, and the composite structure (i.e., paraphragmal areas + phragma 2) is separated from the body of the metanotum by a narrow, transverse membranous area (mem). For clarity, Figure 48 is modified in Figure 49 to contrast internal (apodemal) metanotal areas (stippled in Fig. 49) with external ones. Inserted on the paraphragmal areas are muscles originating on the metasternum and comprising the tergo-sternal indirect flight muscles. The *metapostnotum*



FIGS. **50-51.** *Phanaeus vindex,* male. **50,** pterothorax, lateral view (elytra and coxae in place; mem=intersegmental membrane); **51,** same, ventral view (right coxae removed).

(Figs. 44, 53A, pstn) is reduced to a narrow ridge united with the posterior metanotal margin and bearing phragma 3.

The mesopleura are compressed. The *mesepisterna* (Figs. 50, 52, epis2) form the sides of the projecting mesothoracic rim fitting within the prothorax; basally they are united with the mesosternum. A ridge-like inflection of the anterior margin of each mesepisternum (Fig. 47, imepis) is fused dorsally and ventrally with the mesopleural ridge. On the dorsal end of this inflection is a disc (md) on which originates a muscle inserting on the antero-lateral angle of the mesonotum. The *mesopleural suture* (Fig. 52, pls2) is an impressed, vertical groove separating the mesepisternum and mesepimeron. Its internal invagination is the *mesopleural ridge* (Fig. 47, plrg), the prominent dorsal and ventral ends of which are, respectively, the *mesopleural wing process* (wp2) and *pleural articulation of the mesocoxa* (acx 2). The pleural ridge is the origin of a large muscle inserting on the mesocoxal margin. Each *mesepimeron* has three distinct surfaces, anterior



FIGS. **52-53.** *Phanaeus vindex,* male. **52,** pterothorax, anterior view (elytra and mesocoxae in place; setation shown on right only); **53A,** same, posterior view (elytra and metacoxae removed); **53B,** dorso-posterior angle of metasternum, lateral view.

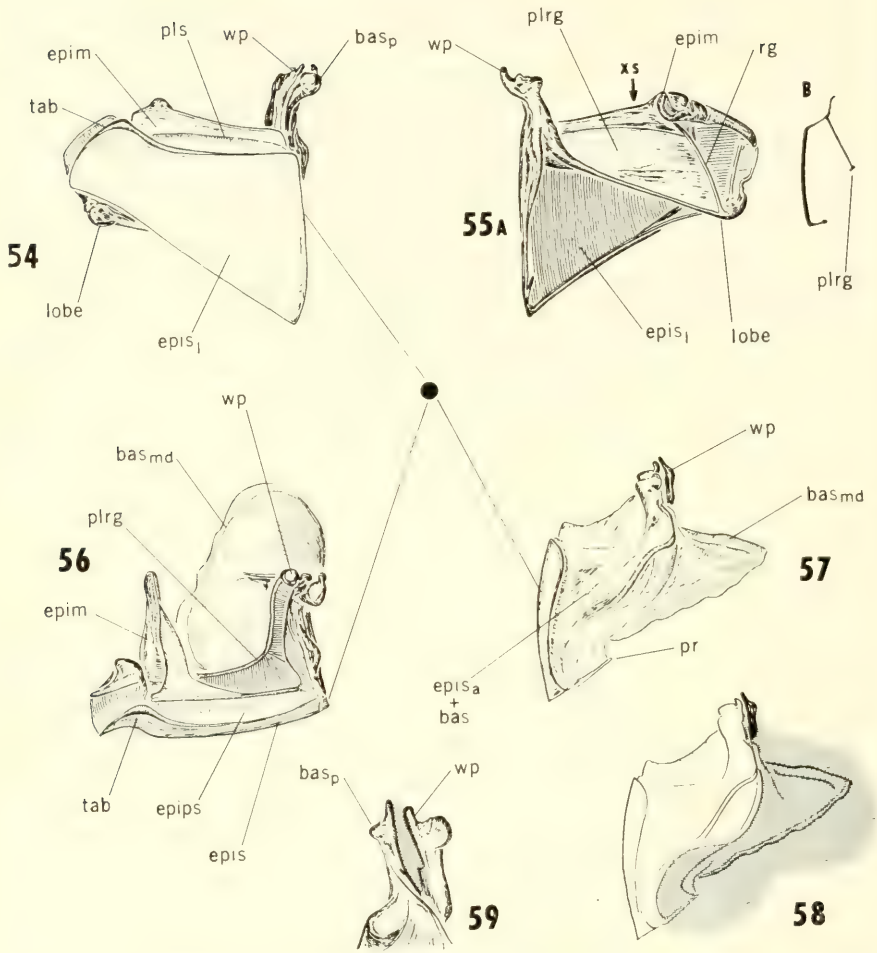
(Fig. 52, epim2_a), lateral (Fig. 50, epim2_l) and posterior (Fig. 47, epim$_p$), which are set off by sharp, vertical bends in the body wall. Of the three, only the lateral surface is permanently exposed and colored and sculptured like adjacent exposed sclerites. The posterior surface is pressed close to the anterior surface, such that in Figure 47 care must be taken to note the vertical posterior margin of the mesepimeron (epim$_{pm}$) to distinguish internal and external surfaces. A smooth, elongate area (y) on the posterior

surface receives the opposing margin of the metepisternum; a similarly smoothed, concave area of the lateral surface (z) contacts the base of the mesocoxa.

The metapleurites are oriented horizontally (see Snodgrass, 1909). The *metepisternum* has two distinct surfaces, anterior (Fig. 57, $epis_a$) and lateral (Figs. 50, 54, $epis3_l$). The lateral surface is trapzoidal, and its dorso-posterior angle (Figs. 54, 56, tab) is produced as a rounded *metepisternal tab* which fits in a depression in the elytral epipleuron. The metepisternal tab is characteristically present in phanaeines. The *metepimeron* (Fig. 54, epim) is a narrow, horizontal sclerite along the dorsal edge of the episternum. It is completely hidden beneath the epipleuron of the closed elytron. Posteriorly, a finger-like portion of the epimeron (Figs. 53A, 56) projects mesally and unites with the lateral extremity of the metapostnotum. Separating the metapleurites is a faint horizontal line, the *metapleural suture* (Fig. 54, pls). Its invagination, the *metapleural ridge* (Fig. 55, plrg) is a very strongly developed, oblique plate; Figure 55B shows the origin of this ridge relative to the metapleurites. The antero-dorsal extremity of the metapleural ridge is the *metapleural wing process* (Figs. 54-57, wp), which supports the second axillary sclerite and base of the Sc vein of the hind wing. Posteriorly the metapleural ridge unites with a vertical ridge (Fig. 55A, rg) supporting the mesal projection of the metepimeron, and the two converge on a rounded lobe (Figs. 54-55, lobe) which inserts in a slot in the dorsal margin of the metasternum. This lobe is not the pleural articulation of the metacoxa. The functional "pleural" or *dorsal articulation of the metacoxa* (Figs. 53A-53B, dacx3) is a tubercle borne on the dorso-posterior angle of the metasternum. Whether or not this tubercle is the dissociated extremity of the pleural ridge or a secondary articular structure is not clear.

The *metabasalare* (Fig. 57, bas) is fused with the anterior surface of the metepisternum, and together the two form an irregular vertical wall fitting against the posterior surface of the mesothorax. The stippled area in Figure 58 (c.f., Fig. 57) is the internal portion of this anterior wall. (In some beetles [e.g., Carabidae] the metabasalare is free, but in Scarabaeidae it is apparently always fused to some degree with the metepisternum [see Snodgrass, 1909].) The apex of the basalare (Fig. 59, bas_p) is elongate and closely associated but not fused to the metapleural wing process (wp); it provides a second fulcral point for the base of vein Sc of the hind wing. Internally the base of the basalare bears an enormous, oval muscle disc (Figs. 56-57, bas_{md}). From this disc extend two muscles, a very large one to the metasternum and a much smaller one to the posterior margin of the metacoxa. Since the basalare is rigidly fused with the body wall, it is quite likely that the basalar-metasternal muscles augment the action of the tergo-sternal indirect flight muscles.

The *mesosternum* (Fig. 51, st2) is a narrow, transverse sclerite between



FIGS. 54-59. *Phanacus vindex*, male. **54,** right metapleuron, lateral view; **55A,** same, internal view (basalare removed; xs=plane of cross section in 55B); **55B,** same, cross section; **56,** same, dorsal view (basal membrane of hind wing removed); **57,** same, anterior view; **58,** same as 57 (stippled area is internal); **59,** apices of metabasalare and metapleural wing process, inner view.

the apices of the mesocoxae. It is convex and bears a transverse, brace (⌒)-shaped ridge which contacts the inflexed posterior margin of the prosternellum. The mesosternum is fused with the median area of the metasternum along the *mesometasternal suture* (sts).

The very large *metasternum* (Fig. 51, st3) forms most of the ventral wall of the pterothorax. It is superficially divided into three parts by the elongate mesocoxae, which rotate in depressions of the metasternum (cxd) similar to

the procoxal depressions of the prosternum. The shape of the median area of the metasternum (between the mesocoxae) is characteristic of phanaeines. Slightly posterior to the mesometasternal suture, it is strongly and abruptly depressed medially as a vertical angulate prominence. Consequently, as seen laterally (Fig. 50), the metasternum is flat and squared anteriorly; seen ventrally (Fig. 51), it is pentagonal and acuminate anteriorly. Since this depression of the median area is normally viewed from below, the metasternum of phanaeines is often described as "raised."

THE PTEROTHORACIC ENDOSKELETON

The pterothoracic structures of interest here are the phragmata and sternal apophyses; other internal skeletal features are discussed above.

Phragma 1 (Figs. 45-46, 52, ph1) is a deeply invaginated plate borne by the anterior margin of the mesonotum. Medially its ventral margin is bent posteriorly, resulting in the bilobed appearance seen anteriorly (Fig. 52). On its anterior surface originate a pair of muscles inserting on the prosternal apophyses; each side of the posterior surface is the origin of two muscles, a large one inserting on the mesocoxal margin and a smaller one on sclerite q. There are apparently no well developed muscles extending between phragmata 1 and 2. *Phragma 2* (Fig. 48, ph2) was mentioned previously.

Phragma 3 (Fig. 53A, ph3) is borne by the metapostnotum. Like phragma 1, it is emarginate medially for passage of the aorta and digestive tract. At the sides of the emargination are two dark, oblique lines which separate a median area; from this area extend short muscles (the dorsal longitudinal indirect flight muscles) to phragma 2. It is noteworthy that these muscles, which effect the downstroke of the wing, are so poorly developed compared to the extensive development of their antagonists, particularly the tergo-sternals and basalar-sternals. From the lateral areas of phragma 3 extend muscles, the "lateral obliques," inserting along the anterior margin of the metascutum. On the *lateral processes of phragma 3* ($ph3_{lp}$) attach muscles from the metafurcal arms that probably stabilize the metafurca.

Both the mesosternal and metasternal apophyses are fused basally. The resulting compound structures, the *mesofurca* and *metafurca,* are quite different in shape. The *base of the mesofurca* (Fig. 52, bfur2) is a transverse, vertical plate marked externally by the mesometasternal suture. In phanaeines and some other scarabaeines, it is braced by a vertical, longitudinal plate, the *mesofurcal brace* (br). The *mesofurcal arms* (afur2) are cup-shaped, opening laterally; within them and on their posterior surfaces originate muscles inserting on the mesocoxal margin. A ribbon-like, lateral extension of each arm (afur2p) serves as the origin of a muscle extending through the coxa and inserting on the base of the trochanter.

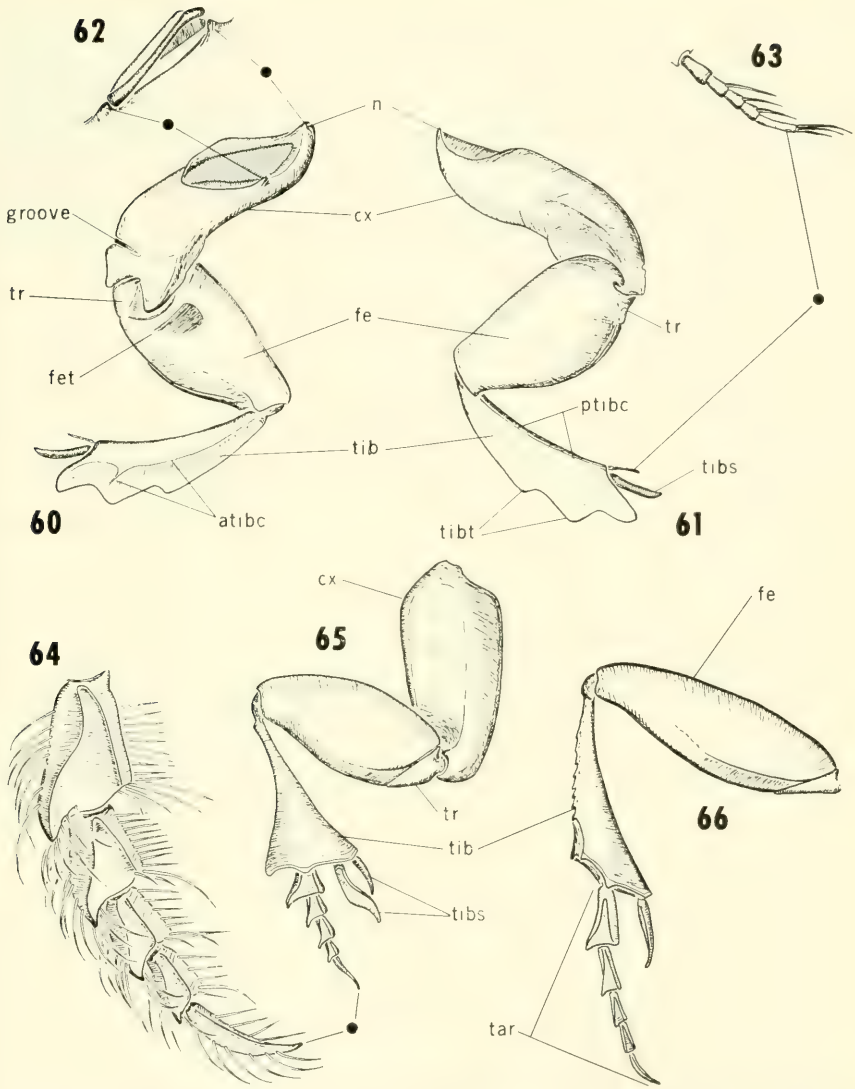
The metafurca (= metendosternite of Crowson, 1938, 1944) is an anteriorly inclined, T-shaped invagination of the metasternum (Fig. 53A). It is borne by a rounded, sternal inflection, the *metafurcasternum,* (fst3), between the bases of the hind coxae. The tubercle on each side of the furcasternum is a *ventral* (sternal) *articulation of the metacoxa* (vacx3). The *base of the metafurca* (bfur3) is elongate and, in cross section, T-shaped (as a steel T-beam). The *metafurcal arms* (afur3) are subapical (the apex of the metafurca is not visible in Fig. 53). On the metafurca, as a whole, originate five pairs of muscles, all of which insert on the metacoxa.

THE LEGS

The fossorial front leg of *vindex* is shown in Figures 60 and 61. The *coxae* (cx) are cylindrical and articulate laterally with the internal, tuberculate *lateral articulation of the procoxa* (Fig. 40, acx), which fits into a small notch (Figs. 60-61, n) in the coxal margin. The concealed *trochantin* (Fig. 62) articulates anteriorly on the coxal margin. The *trochanter* (Figs. 60-61, tr) is fused to the base of the femur and largely hidden in the apex of the coxa; the femur-trochanter line of fusion is visible only posteriorly. The inner margin of the *femur* (fe) is flattened to allow close appression of the tibia. The *profemoral hair plate* (Fig. 60, fet) is a circular group of closely packed, presumably proprioceptive setae on the anterior surface of the femur. When the femur is retracted, this hair plate slips behind the apex of the coxa. The *tibia* (tib) is flattened antero-posteriorly and bears three lateral *protibial teeth* (tibt). The *anterior* (atibc) and *posterior tibial carinae* (ptibc) (Figs. 60-61, respectively) extend the length of the tibia. Abrupt, lateral turns of the anterior carina extend onto the surface of the two distal tibial teeth. In the discussions that follow, tibial teeth bearing such extensions of the anterior tibial carina will be called carinate. A single *protibial spur* (tibs) articulates on the inner apical angle of the tibia; in *vindex* and most other phanaeines, it is pointed and only slightly curved. In other dung beetles, the spurs may show sexual differences (e.g., some *Canthon*) or extraordinary modifications (Onitini), but they are apparently rarely absent.

In most dung beetles *protarsi* are well developed and found in both sexes. In phanaeines, however, they are found only in the females of certain groups, including *Phanaeus,* where they are always reduced in size and clawless (Fig. 63). When present, it inserts on the inner apical angle of the tibia, mesal to the tibial spur. No known male phanaeines possess front tarsi; their curious lack in phanaeines and some other dung beetles has been known for many years (Brullé, 1837; Dejean, 1838).

The middle and hind legs differ principally in length and in articulation and orientation of the coxae. The middle leg (Fig. 65) is shorter and stockier than the hind leg (Fig. 66). The cylindrical *mesocoxae* (Figs. 51,



FIGS. **60-66.** *Phanaeus vindex*, female. **60,** left foreleg, anterior view; **61,** same, posterior view; **62,** trochantin, anterior view; **63,** front tarsus; **64,** right middle tarsus, ventral (= plantar) surface; **65,** right middle leg, ventral view; **66,** right hind leg, ventral view (coxa removed; see Fig. 50). (Setae are shown only in Figs. 63-64.)

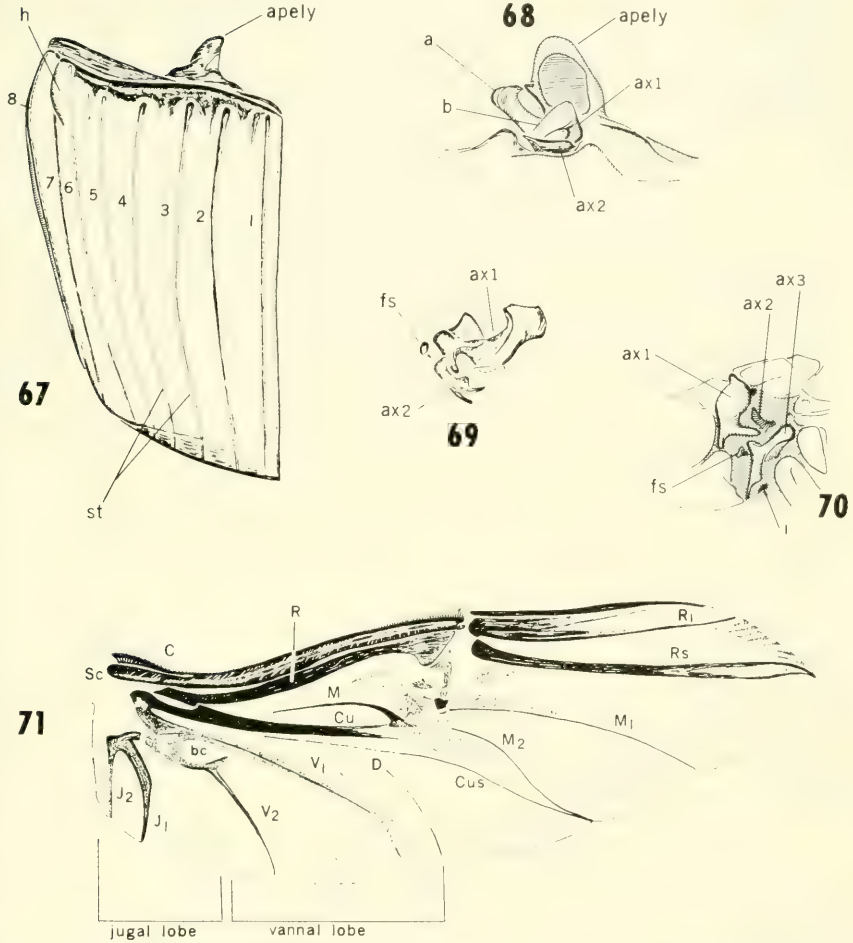
cx2, and 65, cx) are oriented longitudinally and approximately parallel in most phanaeines. The *metacoxae* (Fig. 51, cx3) are elongate and always oriented transversely. The middle coxa has but a single, pleural articulation (to allow rotation along its long axis), while the hind coxa has two. Neither posterior pair of legs has a recognizable trochantin (contrary to Snodgrass,

1909: 563). The trochanter (tr) of both pairs is triangular and fused to the base of the femur. Their femora differ essentially only in length. The tibiae (tib) are only slightly shorter than their respective tarsi. They differ in shape, the middle tibia being round in cross section, the hind tibia being approximately rectangular because of its flattened dorsal surface. The middle tibiae each bear two unequal apical tibial spurs (tibs); each hind tibia, only one. The lateral surface of the hind tibia of a few phanaeines bears a subapical *transverse tibial carina* (Fig. 262, cr), which is absent in *vindex* (Fig. 261). This carina is uncommon in phanaeines but is characteristic of certain other groups, such as *Copris*. Middle and hind tarsi are well developed but always flattened and clawless in phanaeines. Figure 64 is a posterior tarsus of *vindex;* as in all phanaeines, the ventral (plantar) surface of each tarsomere except the last is longitudinally carinate, while the dorsal surface is smooth.

THE WINGS AND THEIR ARTICULATIONS

The *elytra* (Fig. 67; 50, ely) completely cover the metanotum, metepimera and all but the last abdominal terga. The *humeral angle* (h) of each elytron is swollen; beneath it lies the raised base of the folded hind wing. The *elytral epipleuron* (Fig. 50, epip) is the downflexed lateral margin of the elytron; in phanaeines it is narrow. The elytra of phanaeines are held tightly in place when at rest by two complementary mechanisms, namely, by the interlocking grooves in the opposing elytral margins along the elytral suture and by containment of each elytron in the epipleural shelf by the metepisternal tab. The *epipleural shelf* (Fig. 56, epips) is formed by the recessed dorsal margin of the metepisternum, on which rests the epipleuron. The anterior margin of each elytron is strongly downflexed (Fig. 52), forming a vertical wall fitting against the prothorax. The *articular process of the elytron* (Fig. 67, apely) is a lobate extension of the flexed anterior margin. The *elytral striae* (Fig. 67, st) are longitudinal, impressed lines. The elytra of phanaeines each have eight striae, including the often overlooked one (8) adjacent to the epipleuron. The striae are numbered as in Figure 67 (1-8). Each longitudinal zone between two striae is an *interstria* (= interstice, interspace). The interstriae of *vindex* are flat and coarsely rugose (Fig. 284).

There are two *elytral axillary sclerites* (axillaries) beneath the hollowed underside of the articular process of the elytron (Fig. 68). The first (Figs. 68-69, ax1) articulates with both the mesoscutum (at point a in Fig. 68) and the mesopleural wing process (along ridge b). This double articulation suggests that the first axillary is the functional equivalent of the first two axillaries found in other scarabs (e.g., *Phyllophaga;* Snodgrass, 1909), which may be fused in phanaeines. The concave second axillary (ax2) fits over the first and is connected by a membranous thickening with the small *flexor sclerite of the elytron* (Fig. 69, fs), which projects internally as a conical



FIGS. **67-71.** *Phanaeus vindex,* male. **67,** left elytron, dorsal view (strial number, 1-8, to left of corresponding stria); **68,** articular process of elytron and associated elytral axillary sclerites, ventral view (a=lobe of axillary 1 articulating with mesoscutum; b=ridge of axillary 1 articulating on mesopleural wing process); **69,** extracted elytral axillary sclerites, dorsal view; **70,** base of right hind wing and adjacent metanotal area, dorsal view; **71,** right hind wing, dorsal view (bc=basal cell; other symbols indicate veins).

apodeme. Inserted proximally (nearest the body wall) on the flexor apodeme is a thin "tendon" (*no* muscle) originating on an apodeme (Fig. 57, pr) from the lower angle of the metabasalare. Inserting distally is a muscle-bearing, flexible apodeme originating on a process (Fig. 47, pr) from the mesepimeron. The insertions of the direct muscles of the elytron are difficult to trace, but all originate on the mesopleural ridge.

The membranous hind wings are well developed; dung beetles are gen-

erally strong flyers. The reduced venation is of the scarabaeoid type discussed by Stellwaag (1914), Forbes (1922), Graham (1922), d'Orchymont (1920), Balthasar (1942), *et al.,* no two of whom fully agree on vein terminology. The system used here (Fig. 71) is largely a compromise of several systems. The vein and area designations used are not meant to imply homology with those of other insects, including beetles; this terminology is adopted here strictly for comparative purposes within the group.

There are three *axillary sclerites of the hind wing* (Fig. 70). The first (ax1) hinges laterally on the anterior metanotal wing process and articulates anteriorly with the base of vein Sc. The small second axillary (ax2) articulates ventrally on the metapleural wing process. With the wing extended (as in Fig. 70) the apex of the third axillary (ax3) is directed upward, beyond the wing surface. When the wing is flexed, the third axillary rotates on its long axis, the apex swinging mesally to above the posterior metanotal wing process. Mesal to the third axillary and connected to it by a thickening in the basal wing membrane is the *flexor sclerite of the hind wing* (fs). On the flexor sclerite insert all three of the direct flight muscles of the hind wing, two of which originate on the metapleural ridge, the third on the dorsal side of the metabasalar muscle disc.

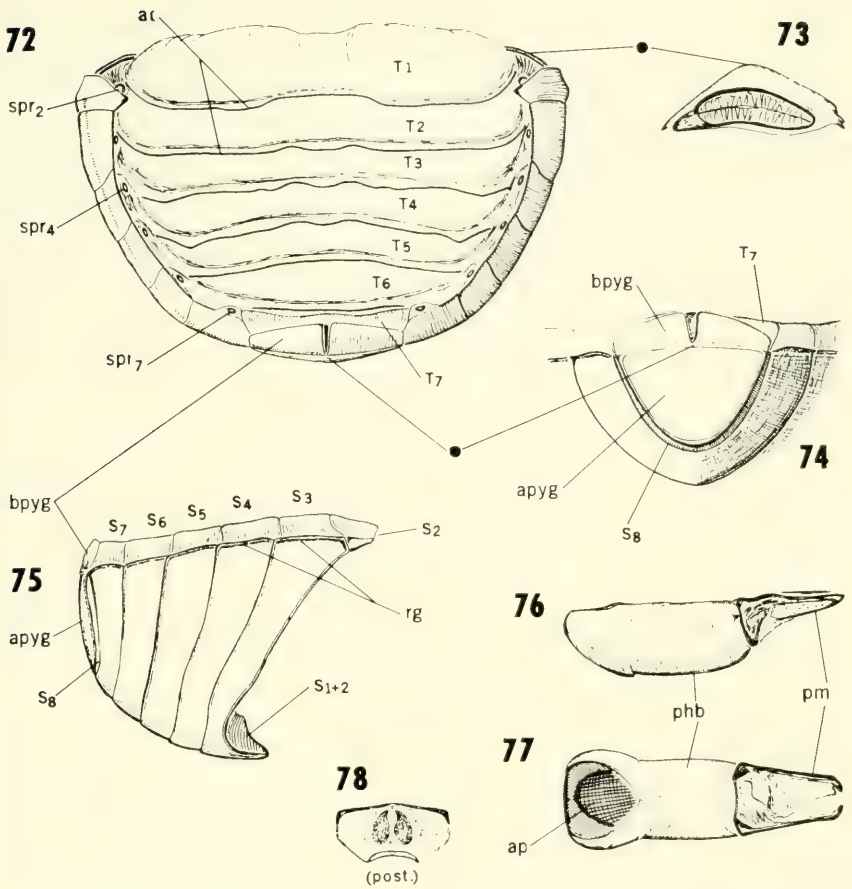
As external sclerites, subalares are lacking in the mesothorax, unless represented by the flexor sclerites. In the metathorax, however, the subalare is definitely represented by a stalked muscle disc (Fig. 53A, $sub3_{md}$) inserted on the basal membrane of the hind wing posterior to the third axillary (point i in Fig. 70). From this disc extends a muscle to the anterior margin of the metacoxa.

THE ABDOMEN

THE ABDOMINAL TERGA

The dorsum of the abdomen is composed of eight terga (Fig. 72, T_{1-7} and pyg). The first seven are covered by the elytra and are thinly sclerotized except for the *acrotergites* (at), thin bands across the anterior margins of each. The ridge-like invagination of each acrotergite is an *antecosta,* an attachment for dorsal longitudinal muscles. The acrotergite of tergum 1 is the metapostnotum; its antecosta, phragma 3. Associated latero-ventrally with each of the first seven terga is a pair of *abdominal spiracles* (spr_{1-7}). With few exceptions, these spiracles of phanaeines are located in the lateral membranous region separating terga and sterna.[8] The large elliptical spiracles of tergum 1 (Fig. 73) open anteriorly; the much smaller succeeding six pairs open dorsally.

[8] This arrangement of abdominal spiracles is characteristic of "Scarabaeidae—Laparosticti," a commonly employed but informal taxonomic division of the family including Scarabaeinae (see Ritcher, 1969b).



FIGS. 72-78. *Phanaeus vindex,* male. **72,** abdomen, dorsal view; **73,** first abdominal spiracle, anterior view; **74,** abdomen, caudal view; **75,** same, lateral view (terga 1-7 removed); **76,** genital capsule, lateral view; **77,** same, dorsal view; **78,** ninth sternum, ventral view (post. indicates posterior margin).

The last (eighth) abdominal tergum, or *pygidium,* is a thickly sclerotized, vertical plate covering the anal and genital openings[9]; it is only partially covered by the elytra. The covered portion, the *base of the pygidium* (Figs. 72, 74-75, bpyg) is short and grooved medially. The permanently exposed *apex of the pygidium* (apyg) is rounded and, in phanaeines, bears a continuous, unbroken raised margin.

[9] The suggestion arises that the pygidium comprises two terga, 8 and 9; however, a critical study of the musculature of the pygidium and adjacent structures (which is quite intricate) is in order before the possibility can be seriously considered.

THE ABDOMINAL STERNA

The abdominal venter is composed of eight sterna in the female, nine in the male. The first two (Figs. 51, 75, S_{1+2}) are inflexed behind the metacoxae and, except for the dorso-lateral extremities of the second, permanently hidden.[10] Sterna 3-8 are ventrally exposed (Fig. 75, S_{3-8}). Although clearly separated by impressed lines, they are rigidly fused. Sterna 1-3 are acutely produced antero-medially between the apices of the metacoxae (Figs. 51, 75) and form a prominence fitting against the metafurcasternum. The dorso-lateral extremities of sterna 2-7 (= abdominal pleurites of authors) are impressed and covered by the elytra. Longitudinal ridges (Fig. 75, rg) separate these impressed areas from the ventral portions. The dorso-lateral extremities of sternum 8 are acute and do not extend beneath the elytra.

Sternum 9 (Fig. 78) is found only in the male. It is a thinly sclerotized, internal plate (i.e., "cryptosternite") fitting beneath the apex of the genital capsule. Though no such plate is present in the female, it may be represented by a pair of poorly sclerotized plates below the opening of the common oviduct.

EXTERNAL GENITALIA

The male intromittant organ is enclosed in the *genital capsule* (Figs. 76-77), which consists of an elongate tube, the *phallobase* (phb), bearing apically a pair of lateral appendages, the *parameres* (pm). Within the phallobase is a well developed, membranous lobe, the *aedeagus,* which is presumably extruded from the phallobase between the movable parameres during copulation. Basally the aedeagus bears a large *aedeagal apodeme* (ap), on which insert the retractor muscles of the aedeagus. Sclerotized external genitalic structures exist only in the male of dung beetles. The terminology applied here is that of Snodgrass (1957). It differs considerably from that commonly applied in beetle taxonomy, in which, for example, the genital capsule is often referred to as the aedeagus, and the present aedeagus as the median lobe, phallus or penis. Lindroth (1957) has reviewed the various terminologies applied to beetle genitalia.

PART III: COMPARATIVE SKELETAL MORPHOLOGY OF PHANAEINES

The purpose of this part is to present a resumé of the morphological variation largely upon which is based the classification proposed in part V and the evolutionary discussion in part VI. In addition, this section intro-

[10] The second abdominal sternum, when exposed only dorso-laterally, characterizes the haplogastran type beetle abdomen; Jeannel and Paulian (1944) stressed this character when grouping Scarabaeoidea and Staphylinoidea as the suborder Haplogastra (but see Crowson, 1955).

duces some characters which, to my knowledge, have heretofore not been discussed in systematic studies of Scarabaeinae.

The characters treated here are admittedly only a small portion of those potentially available from an unlimited study of dung beetle skeletal morphology. Practicality, however, demands adoption of some reasonable criteria to limit them to a manageable number, which, unless computer techniques are used, is apt to be quite small. The following criteria were stressed in selecting characters discussed below:

(1) that they (the characters) be supraspecific characters; that is, that their variation in general be less within a species group (or higher category) than among several. This criterion, however, does not strictly limit characters to those with wide taxonomic application since some character states may be constant only among the species of a single taxon while varying widely among the species of other taxa of similar size or rank;

(2) that as nearly as possible they represent all tagmata and appendages;

(3) that they be studied in at least one representative species of each recognized supraspecific taxon;

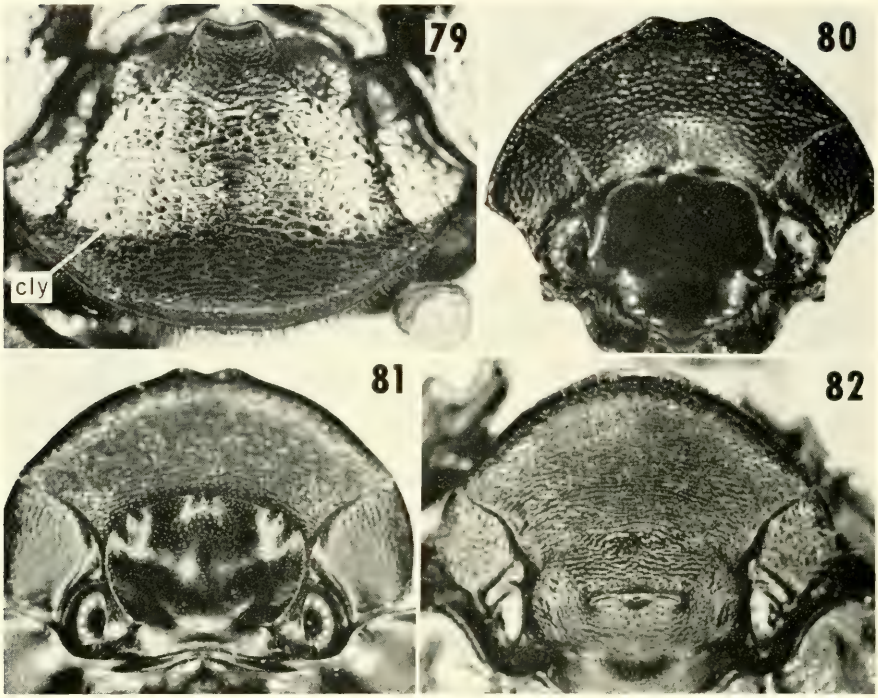
(4) that they not require extensive quantitative analysis. This restriction was imposed primarily because of the lack of series of a sufficiently diverse group of representative species large enough to support a reasonable degree of quantitative rigor;

(5) that, except in cases of monobasic genera, they not be characters unique to single species.

Even though most are easily observed, characters were not avoided because they require special effort to assess.

About 90% of all known species representing all phanaeine genera were examined during the course of this study, including most of the rarer ones. However, not all species were examined with the same thoroughness; the appendix indicates the extent to which each was examined. Since a revision of species is not the present problem, no special effort was made to obtain large series (more than 20 individuals). Such large series were studied in some instances only to aid in determining what characters tended to vary greatly intraspecifically. Except in cases of extremely rare species (e.g., *Homalotarsus impressus*), the minimum number of specimens examined of each was an individual of each sex; usually more specimens were available.

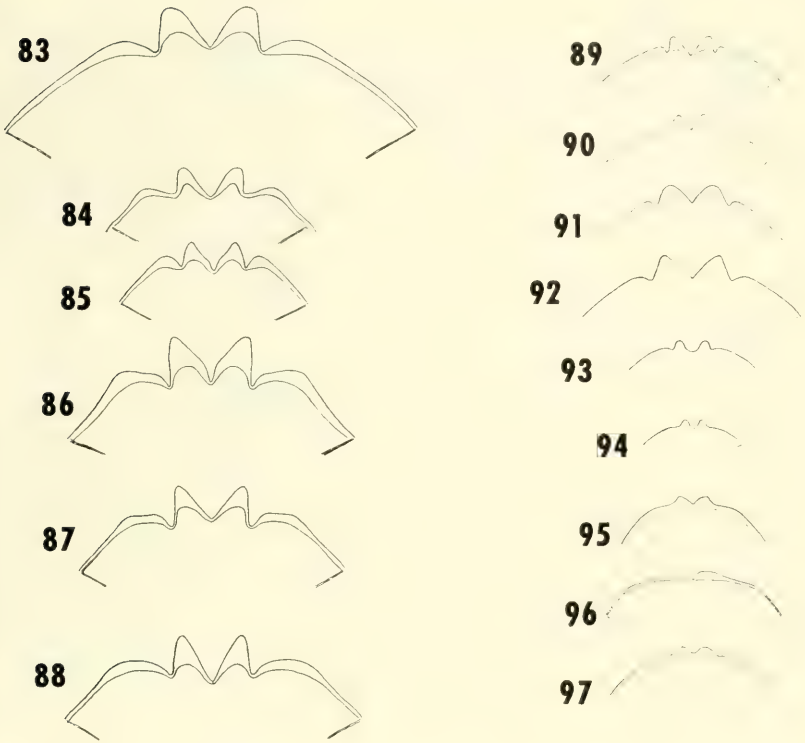
In general, the sequence of characters treated here is the same as in the foregoing section. The name of some characters is preceded by a number (1-22) to permit easy cross reference in following sections. In a few instances (e.g., character 6) certain highly correlated features are treated together even though they may be in quite distinct anatomical locations. Numbered characters are "generic characters" in that they generally have wide taxonomic application at the genus level; hence, they form the nucleus



FIGS. 79-82. **79,** *Phanaeus vindex*, female, frontal view of head; **80,** *Oxysternon curvispinum*, male, dorsal view of head; **81,** *Phanaeus haroldi*, female, dorsal view of head; **82,** *P. melampus*, female, dorsal view of head.

of the generic descriptions given below. It should be said, however, that description of genera is limited neither to states of these numbered characters nor to the variation discussed in this section.

The states of many characters are designated by a, b, etc. In these instances the discussion of each state of the character is introduced by a few "key" words followed, if necessary, by a complete description of the state. For brevity, these key words, which are not necessarily self-explanatory, will be used in subsequent discussions (keys, descriptions, etc.). If a given character state is reasonably regularly distributed at or above the subgenus level, its definition is followed by the names of those taxa possessing it. For this purpose, it is necessary to use names not formally introduced and defined until later; to gain some taxonomic perspective, one can refer to the classification outline presented at the beginning of Part V. Names of taxa used in this section may be followed by (ex) or (inf). When (ex), exception(s), is noted, one or more species (but usually only a small percentage of all species) of the cited taxon possess another defined state; unless they are pertinent to the discussion of the character, these exceptional species



FIGS. 83-97. Anterior clypeal margins, dorsal views. 83, *Coprophanaeus lancifer;* 84, *C. pertyi;* 85, *C. saphirinus;* 86, *C. dardanus;* 87, *C. pluto;* 88, *C. jasius;* 89, *Dendropaemon renatii;* 90, *D. viridis;* 91, *D. ganglbaueri;* 92, *D. amyntas;* 93, *D. bahianus?* 94, *D. denticollis;* 95, *Tetramereia convexa;* 96, *Megatharsis buckleyi;* 97, *Homalotarsus impressus.*

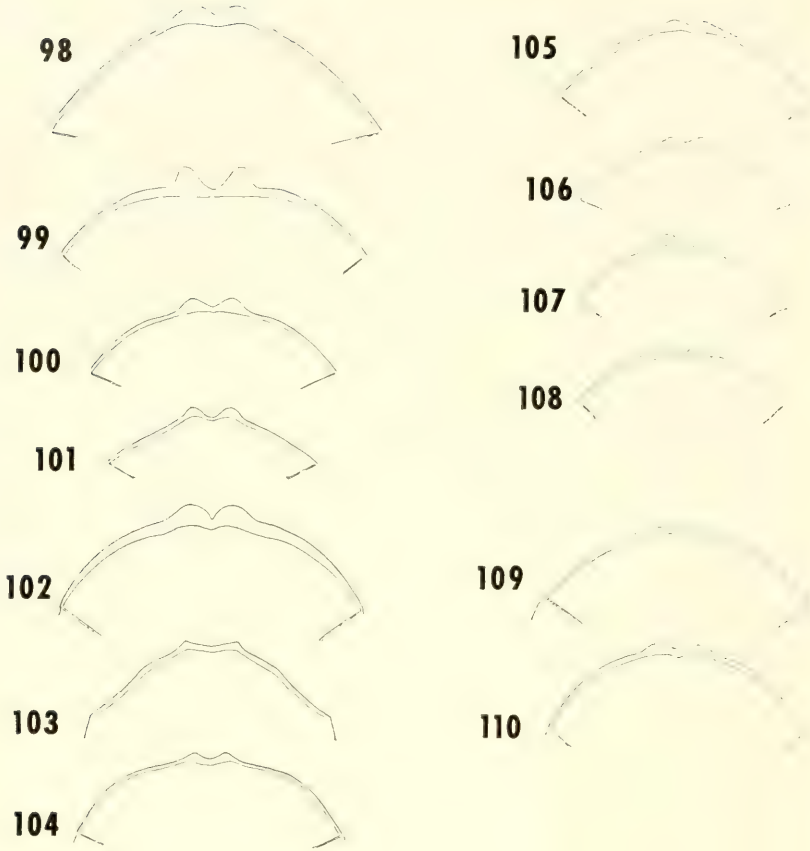
are not mentioned. When (inf), inferred, is noted, the character state in question is one requiring dissection to observe, for which expendable material of the cited taxon was not available.

Discussion of some characters is omitted from this part. Those concerning color and size will be mentioned in the systematic section. For comparison of the genital capsules of males, which were not examined for this study, the reader is referred to Olsoufieff's monograph (1924), particularly to Plates III-VII which illustrate the genital capsules of a large number of phanaeines.

THE HEAD CAPSULE

Various aspects of the variation in structure of the head capsule provide important taxonomic characters at supraspecific levels.

CLYPEAL SCULPTURING: The entire dorsal surface of the clypeus of most phanaeines is completely transversely ridged (Figs. 79, 82). In some species

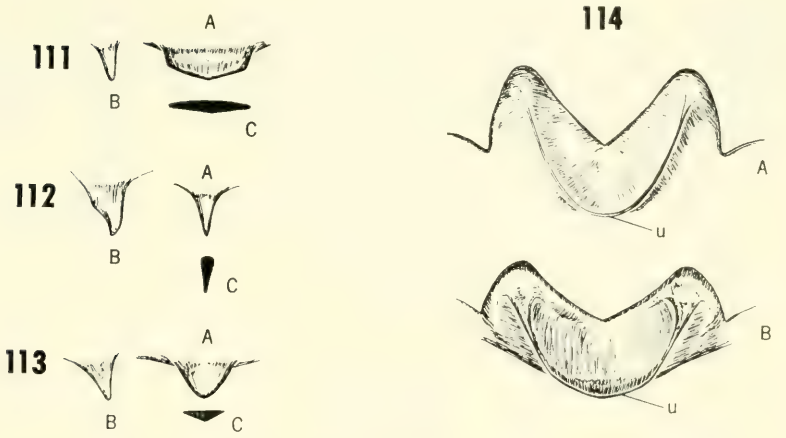


FIGS. **98-110.** Anterior clypeal margins, dorsal views. **98,** *Diabroctis mimas;* **99,** *D. mirabilis;* **100,** *Oxysternon conspicillatum;* **101,** *O. palaemon;* **102,** *Sulcophanaeus imperator;* **103,** *S. velutinus;* **104,** *S. carnifex;* **105,** *S. menelas;* **106,** *Phanaeus splendidulus;* **107,** *P. endymion;* **108,** *P. palaeno;* **109,** *P. demon;* **110,** *P. amethystinus.*

of *Oxysternon* (including all *Mioxysternon,* Fig. 80) and in isolated species in other genera it is punctate posteriorly.

1. SHAPE OF THE ANTERIOR MARGIN OF THE CLYPEUS.

a. emarginate medially—interrupted medially by three (rarely one, Fig. 90) usually acute emarginations, middle one being deepest; emarginations setting off two large, acute median teeth (Figs. 83-89, 91-92). *Coprophanaeus, Dendropaemon.* In some species of *Dendropaemon* the clypeal teeth and emarginations are rounded (Figs. 93-94). The emarginate clypeus is usually coincident with the U-shaped clypeal process (see character 2a, below).



FIGS. **111-114.** Clypeal processes, A—frontal view, B—lateral view, C—cross section. **111,** *Phanaeus mexicanus;* **112,** *Oxysternon conspicillatum;* **113,** *Sulcophanaeus faunus;* **114,** *Coprophanaeus spitzi* (A—ventral view; B—frontal view).

b. not emarginate medially—not interrupted medially by acute emarginations; medially rounded (Fig. 109) or distinctly bidentate (Figs. 95-108, 110). All other genera not mentioned in a. This state is coincident with clypeal processes of several types (character 2, b-d) but never with a U-shaped process.

Character 1 is the first of several (see section on phylogeny) indicating a presumed phyletic separation of *Coprophanaeus* and *Phanaeus* (and allied genera). At least in *Coprophanaeus* an emarginate clypeus, strengthened by a unique U-shaped clypeal process, as well as strongly toothed front tibiae (see character 18) are probably related to necrophagy (see part IV). The unique clypeal (and tibial) dentition of *Coprophanaeus* is approached by *Phanaeus endymion* and closely related species (Figs. 108, 256).

2. CLYPEAL PROCESS:

a. U-shaped—curved ridge extending onto ventral surfaces of median clypeal teeth (Fig. 114, u). *Coprophanaeus, Dendropaemon.* Although usually distinct, the process of *Dendropaemon* is only weakly produced.

b. transverse—straight, transverse ridge usually wider than high (Figs. 9-10, clypr; 111) but sometimes tooth-like (Fig. 113) or acute. *Diabroctis, Sulcophanaeus, Phanaeus* (ex), *Mioxysternon* (very weakly produced).

c. spiniform—laterally compressed, acute spine (Fig. 112). Some *Oxysternon, sen. str.*

d. reduced—no distinct ridge, etc., present; process at most represented by a weak gibbossity, raised area or poorly defined ridge. *Tetramereia, Homalotarsus, Megatharsis.* In all three genera the ventral surface of the

clypeus is strongly swollen in the area occupied by the clypeal process in other groups; this swelling is similar to that bearing the U-shaped process.

It should be noted that since the head functions as a digging instrument, such features as the anterior margin of the clypeus and clypeal processes are subject to wear which can alter their shape.

LATERAL CLYPEAL CARINAE: These ridges are usually present although their extent and distinctness is subject to variation which cannot meaningfully be partitioned into states. These carinae are characteristically absent in only a few supraspecific taxa (*Mioxysternon, Tetramereia* and *Homalotarsus*) as well as isolated species in nearly all other groups.

The TRANSVERSE CLYPEAL CARINA is unique among phanaeines to *Diabroctis* (Figs. 194, 197, tcrcly); a similar carina is characteristic of *Onthophagus* (Onthophagini).

3. CEPHALIC PROCESS OF THE MALE: The shape of the male cephalic process varies greatly among species, in addition to intraspecific allometric variation. The following three types are the most common; they do not represent mutually exclusive groups since intermediate and unique types are not considered. Except when otherwise indicated, the following apply only to large, well developed ("major") individuals; the type of process borne by smaller ("minor") individuals, while reduced in size, is usually recognizable.

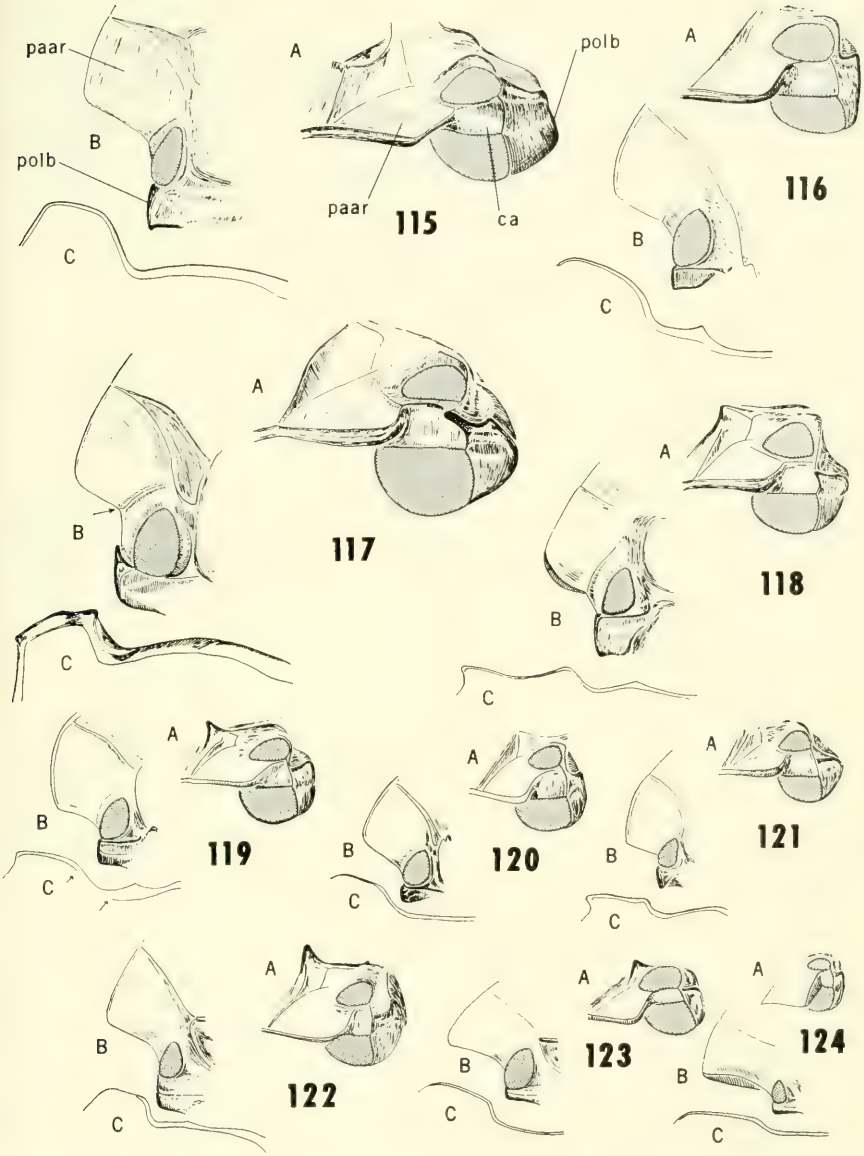
a. lamellate—antero-posteriorly flattened process with or without two or three distal projections of equal or unequal size and shape; usually presenting flattened anterior surface (Figs. 186, 188, 192-193, 305). This type is characteristic of *Coprophanaeus, sen. str.,* some *Dendropaemon,* and *Diabroctis mimas* and *cadmus.*

b. carinate—a transverse carina, wider than high. Most *Dendropaemon, Tetramereia, Homalotarsus* (inf), *Megatharsis* (inf).

c. corniform—a long, usually gradually tapering "horn" erect or curving posteriorly over pronotum (Figs. 1, 181, 183, 189, 198, 203-204, 209-211, 216, 218, 221, 226). This is by far the most common type and only type found in large males of the following taxa: *Sulcophanaeus, Oxysternon, sen. str., Phanaeus, Megaphanaeus, Metallophanaeus.* In small males of *Oxysternon, sen. str.,* all *Mioxysternon* and two *Phanaeus* (*palaeno* and *kirbyi*) the process is reduced to a pair of closely set, median tubercles (Fig. 80).

4. CEPHALIC PROCESS OF THE FEMALE: In general, the female cephalic process is subject to much less interspecific and intraspecific variation than is that of the male.

a. corniform—a long, tapering "horn" (Figs. 182, 199) or large, horn-like process (Fig. 201). This is an uncommon condition among phanaeines and other dung beetles; in general, these females are of species the males of



FIGS. **115-124.** Head and prothoracic structure; A—lateral view of head region around eye, B—same, dorsal view, C—left side of anterior portion of pronotal margin, dorsal view. **115,** *Diabroctis mimas;* **116,** *Coprophanaeus jasius;* **117,** *Sulcophanaeus faunus;* **118,** *Oxysternon conspicillatum;* **119,** *Phanaeus haroldi;* **120,** *Coprophanaeus saphirinus;* **121,** *Sulcophanaeus chryseicollis;* **122,** *S. imperator;* **123,** *Dendropaemon renatii;* **124,** *D. fractipes.*

which also have corniform processes; since the pronotal structure of the female is usually also masculine, the sexes tend to closely resemble each other in general appearance. Corniform or corniform-like processes are characteristic of *Megaphanaeus* and the *faunus* group of *Sulcophanaeus*.

b. carinate—a straight or anteriorly bowed, transverse carina, usually trituberculate (Figs. 81, 185, 197, 207, 213). This is the usual type of process in phanaeines and other dung beetles; it is characteristic of all phanaeine taxa except those mentioned above. In many species of *Phanaeus* it is a short thickened ridge which is more-or-less isolated between the eyes (Fig. 82) and, in a few species (e.g., *vindex*, Figs. 3, 79), distinctly raised.

PARAOCULAR AREAS OF THE PARIETALS: These vary in many respects, among them sculpturing (smooth to strongly rugose) and relief. In *Dendropaemon* they are always strongly raised medially (above) as a large bump or thick transverse ridge (Fig. 134); they are flat in *Tetramereia, Homalotarsus* and *Megatharsis*. In other taxa they vary among species (convex, flat or concave). In most phanaeines the paraocular areas are carinate lateral to the upper portion of the eye; this carina is characteristically lacking in few multispecific taxa (e.g., *Coprophanaeus, sen. str.*). These areas also vary in width, the basis of the following character:

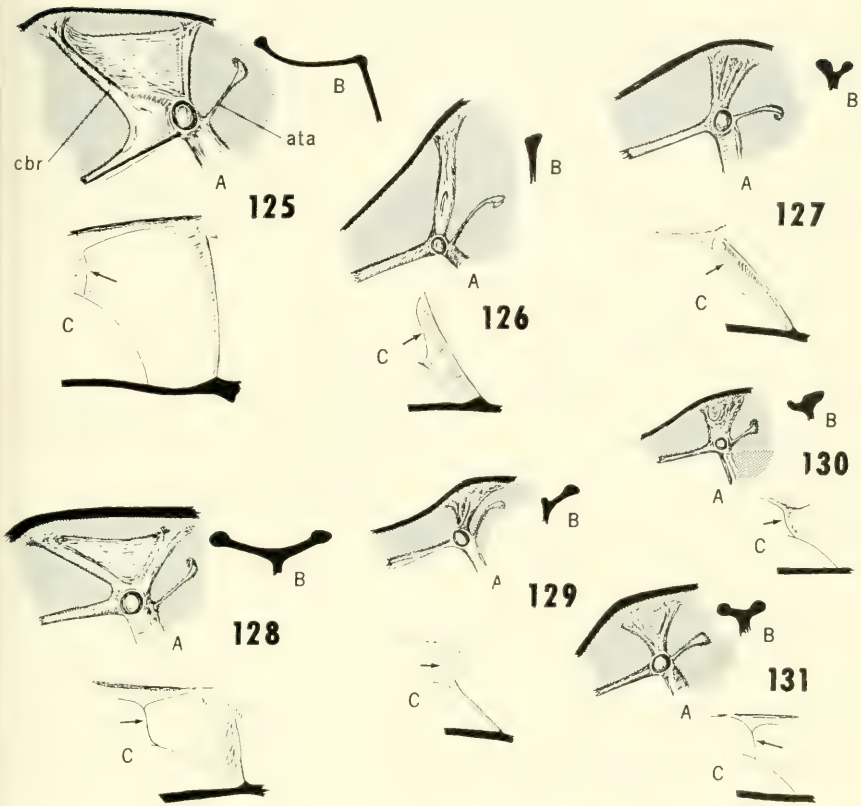
5. WIDTH OF THE PARAOCULAR AREAS:

a. narrow—width of area, along its posterior margin, less than three times (usually about two times) width of adjacent dorsal portion of eye (Figs. 115B-123B). All taxa except those mentioned in b.

b. wide—width at least three times (usually more) width of eye (Figs. 124B, 134-135). *Dendropaemon, sen. str.*, (ex), *Tetramereia, Homalotarsus, Megatharsis*.

6. POSTOCULAR LOBES OF THE PARIETALS: The shape of the posterior portion of the head capsule varies in a number of rather subtle ways, most of which indicate no regular taxonomic pattern. The most easily described of these variables is the angle at which the postocular lobes of the parietals are depressed posterior to the dorsal portions of the eyes (as seen dorsally). Although intermediates occur, the state of the members of most taxa is clearly one of two extremes, each correlated with a distinct shape of the anterior portion of the circumnotal ridge:

a. depressed transversely—lobes depressed straight behind eyes in plane perpendicular to long axis of body (Figs. 115B-117B, 120B-124B); anterior portion of circumnotal ridge not broken by emarginations receiving the postocular lobes (same Figs., C). All genera except *Phanaeus* and *Oxysternon*. In the *dardanus* group of *Coprophanaeus, sen. str.*, the circumnotal ridge is effaced behind the eyes but not distinctly emarginate. In all *Copro-*



Figs. 125-131. Head structure: A—inner view of cephalic brachium and adjacent structures (stippling indicates surrounding intracephalic space), B—cross section through brachium, C—outer view of head wall in region of mesal branch of fronto-clypeal sulcus (indicated by an arrow). **125,** *Sulcophanaeus faunus;* **126,** *Coprophanaeus jasius;* **127,** *Phanaeus demon* (female); **128,** *Oxysternon conspicillatum;* **129,** *O. palaemon;* **130,** *Phanaeus palaeno;* **131,** *P. chalcomelas.*

phanaeus and *Dendropaemon* the postocular lobes are conspicuously flattened behind (compare polb in Figs. 115A and 116A).

b. depressed obliquely—lobes depressed behind eyes in plane oblique to long axis of body; depressions setting off prominent, posteriorly directed portions of the lobes (Fig. 4) received by distinct emarginations (Fig. 35, emarg) interrupting anterior position of circumnotal ridge. *Phanaeus* (ex).

Oxysternon, sen. str., characteristically shows a state intermediate to a. and b. above (Fig. 118); the circumnotal margin, while usually weakened by shallow emarginations, is not always distinctly broken; in *Mioxysternon* the entire anterior portion of the circumnotal ridge is effaced.

CANTHAL AREA: The shape and extent of this area varies more or less continuously with most taxa possessing one of two extremes:

a. distinct—posterior margin of paraocular area (as seen dorsally) approaching middle of eye, leaving, as seen laterally, a flattened or concave canthal area (Figs. 115A, ca, 116A-118A, 121A-124A) between upper and lower portions of eye. Most members of all taxa except *Phanaeus* and *Mioxysternon*.

b. indistinct—posterior margin of paraocular area approaching posterior angle of eye, not leaving a distinct canthal area (Figs. 1, 4). *Mioxysternon* and *Phanaeus*.

Figure 120A shows an intermediate state.

7. SHAPE OF CEPHALIC BRACHIUM:

a. bipodal—presenting two distinct "arms" (Figs. 5, cbr; 128, 131); mesal branch of fronto-clypeal sulcus Y- or T-shaped (Fig. 1, mbfcs). *Phanaeus, Oxysternon, sen. str., Mioxysternon* (inf). In a few species of both genera the bipodal nature is obscured by a presumed reduction in size of one or both "arms" (Figs. 127A, 129A, 130A) and coincident shortening or loss of the anterior extension of the sulcus (same Figs., C); in these cases only cross sections of the respective brachia (same Figs., B) show that they are bipodal.

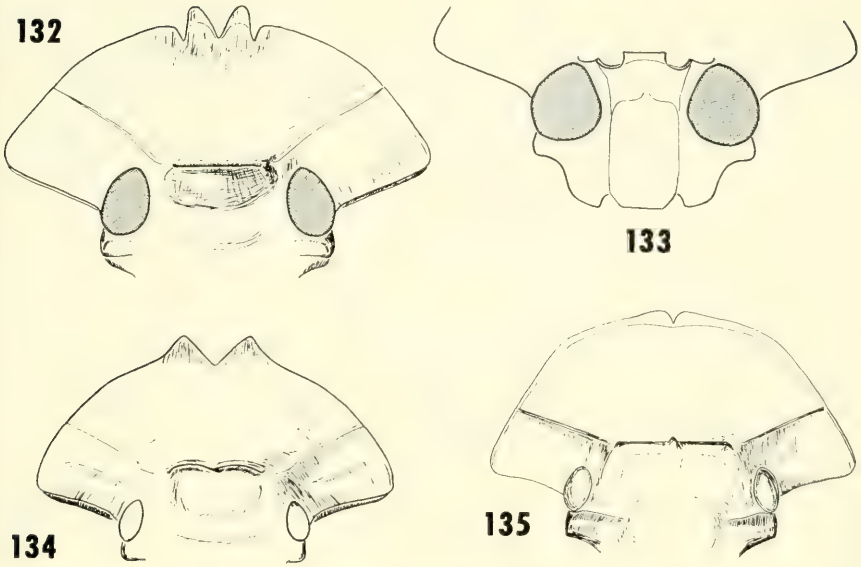
b. monopodal—presenting a single, usually straight and vertical "arm" (Fig. 126A); mesal branch of fronto-clypeal sulcus not forked, usually straight (Fig. 126C). All genera except *Phanaeus* and *Oxysternon;* inferred for *Homalotarsus*. The brachia of *Sulcophanaeus faunus* (Fig. 125A) and *S. carnifex* are apparently unique monopodal types which appear superficially as bipodal (a few *Sulcophanaeus* do have bipodal brachia). As indicated by the course of the mesal branch of the fronto-clypeal sulcus (Fig. 125C) and cross section of the brachium (Fig. 125B), the brachium of these species is a single, anteriorly bent vertical plate.

Since the shape (forked or not) of the mesal branch of the fronto-clypeal sulcus can be considered a projection of a cross section of the brachium, type of brachium can usually be determined accurately without internal examination. The sulcus is regularly obscured only in the *auricollis* group of *Sulcophanaeus*.

8. SIZE OF EYES:

a. small—dorsal interocular width more than four times width of dorsal portion of an eye (Figs. 4, 134-135); width of lower portion of an eye less than twice (usually about equal) width of adjacent oculo-gular space (Fig. 9). With few rare exceptions, all taxa except *Megaphanaeus, Coprophanaeus, sen. str.,* and *Coprophanaeoides*.

b. large—dorsal interocular width less than four times width of dorsal portion of an eye (Fig. 132); width of lower portion of an eye at least twice



FIGS. **132-135.** **132,** *Dendropaemon renatii,* dorsal view of anterior portion of head; **133,** same, ventral view of posterior portion of head; **134,** *D. viridis,* dorsal view of anterior portion of head; **135,** *Megatharsis buckleyi,* dorsal view of anterior portion of head.

(usually more) width of adjacent oculo-gular space (Fig. 133). *Megaphanaeus, Coprophanaeus, sen. str.* and *Coprophanaeoides.*

9. OCCIPITAL RIDGE:

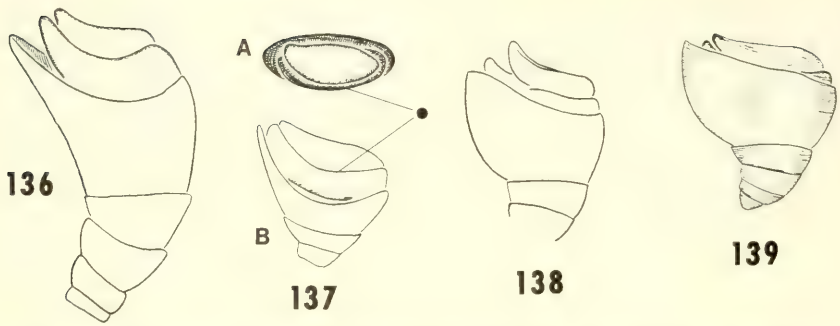
a. complete—usually setose ridge extending dorsally over posterior position of head (Fig. 1, 4, 8, ocr); small medial section occasionally obscured by punctures. *Oxysternon, Phanaeus.*

b. incomplete—ridge absent or, at most, represented by usually weak lateral segments, never distinct dorsally. All genera except *Oxysternon* and *Phanaeus.*

In all phanaeines except *Megaphanaeus* the occipital areas are flattened or weakly concave; in this subgenus, however, the areas are abruptly raised postero-laterally as prominent bumps, anterior to which they are strongly concave.

APPENDAGES OF THE HEAD

ANTENNAE: The antennae are subject to some subtle variation which is exceedingly difficult to render as distinct character states without the use of statistical procedures (e.g., relative lengths of antennomeres, etc.); very little antennal variation is striking enough to assess otherwise. Noteworthy among this latter variation is the tendency in *Dendropaemon* for elongation of first



FIGS. 136-139. **136,** *Dendropaemon fractipes,* flagellum of right antenna, dorsal view; **137,** *D. denticollis,* A—apical view of left antennal club, B—apical five segments of left antenna, ventral view; **138,** *Homalotarsus impressus,* apical five segments of right antenna, dorsal view; **139,** *Megatharsis buckleyi,* flagellum of right antenna, dorsal view.

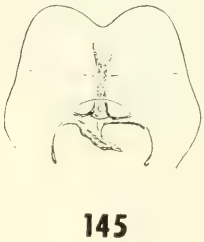
lamella (Fig. 136) and dorso-ventral flattening of the entire club (Fig. 137) and the near hemispherical club of *Megatharsis* (Fig. 139) and *Homalotarsus* (Fig. 138).

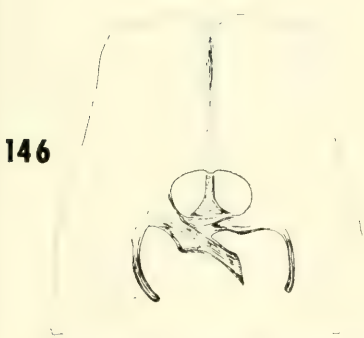
LABRUM: Variation in the labrum offers a number of important taxonomic characters, both unique to few taxa and with wide application. Among the unique features are two characteristic only of *Dendropaemon:* (1) apical margin deeply emarginate (Fig. 145) (that of other phanaeines may be weakly emarginate), and (2) antero-median process of suspensorium forked anteriorly, within fork insert setae of median brush (Fig. 145). Labral characters of potential significance which were not studied include various aspects of chaetotaxy (e.g., number of setae in lateral files); study of these was not approached since their efficient interpretation would have required statistical methods (see introduction to this part).

One of the principal aspects of labral variation is the definition of two principal labral types based on the correlation of three characters: lateral files, type of median brush and type of labral suspensorium.

10. LABRAL TYPE:

a. *Coprophanaeus*-type—lateral files of labrum parallel or nearly so (divergent in *Coprophanaeus*), distance between anterior ends less than 1.25 (usually about 1.0) times distance between posterior ends (Figs. 140, 142, 144); central setae of median brush much longer than setae posterior to them (Fig. 148) or median brush comprising only few, very long setae (Fig. 144); length of opening in suspensorium 0.5 times or less length of dorsal surface of labrum, opening usually very transverse, tormal arms narrow and often converging posteriorly (Figs. 141, 143, 145-146). *Coprophanaeus, Homalotarsus* (inf), *Tetramereia, Megatharsis, Dendropaemon.* These

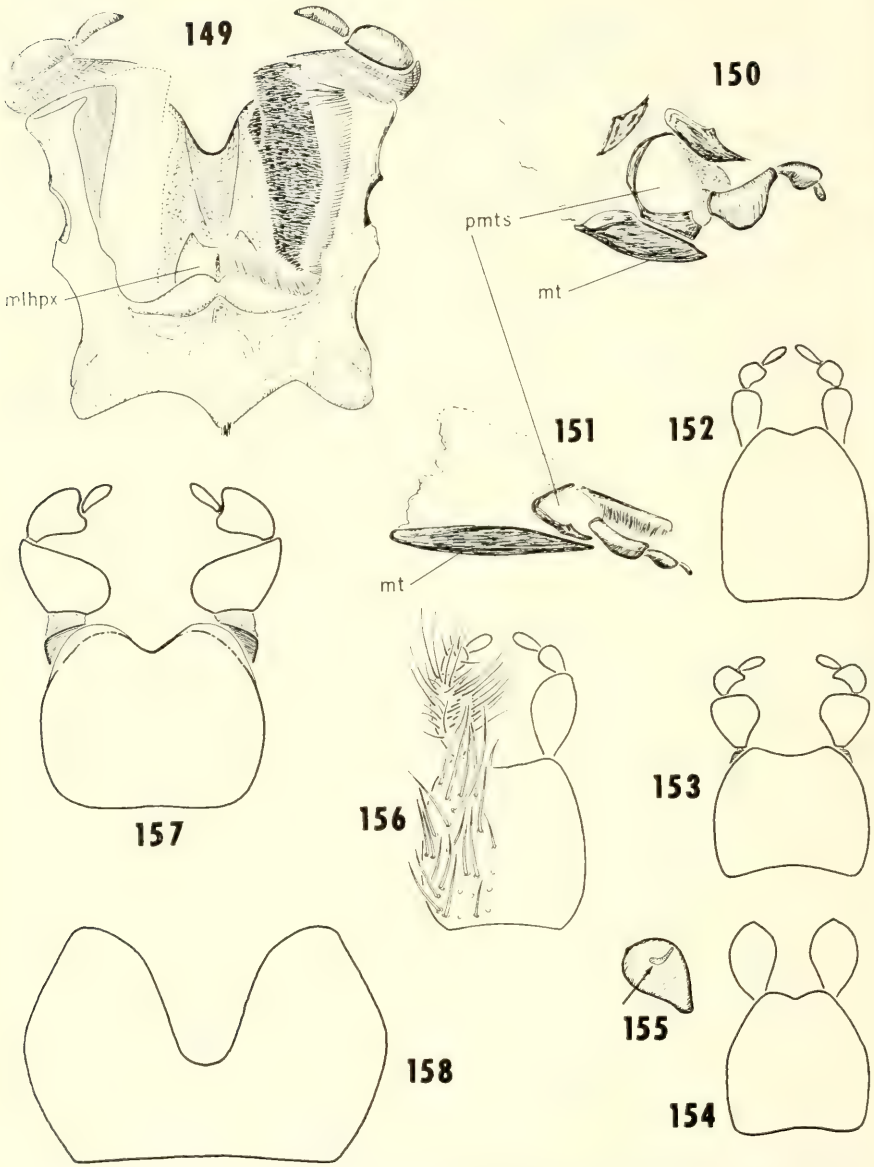




FIGS. **140-148.** Labra. **140,** *Megatharsis buckleyi,* ventral view; **141,** same, dorsal view; **142,** *Tetramereia convexa,* ventral view; **143,** same, dorsal view; **144,** *Dendropaemon viridis,* ventral view; **145,** same, dorsal view; **146,** *Coprophanaeus jasius,* dorsal view; **147,** same, ventral view; **148,** same, lateral view of median brush of labrum.

genera, in the foregoing order, show progressively a reduction in the number of setae comprising the median brush, from a large number in *Coprophanaeus* to a few in *Dendropaemon;* the labral suspensorium of the last four genera is weakly sclerotized compared to that of other phanaeines.

b. *Phanaeus*-type—lateral files divergent, distance between anterior ends more than 1.25 (usually about 1.5) times distance between posterior ends (Figs. 19A, 147); central setae of median brush not much longer than setae posterior to them (Fig. 18), brush never reduced to a few setae, long or



FIGS. **149-158. 149,** *Sulcophanaeus batesi,* dorsal view of labium (floor of buccal cavity not shown); **150,** same, lateral view (slightly smaller scale than Fig. 149; only apical portion shown in detail); **151,** *Dendropaemon viridis,* lateral view of labium (only apical portion shown in detail); **152,** same, ventral view of mentum and palpi; **153,** *Tetramereia convexa,* ventral view of mentum and palpi; **154,** *Megatharsis buckleyi,* ventral view of mentum and palpi; **155,** same, dorsal view of right palpus; **156,** *Homalotarsus impressus,* ventral view of mentum and palpi; **157,** *Coprophanaeus jasius,* ventral view of mentum and palpi; **158,** *Sulcophanaeus faunus,* ventral view of mentum.

not; length of opening in suspensorium more than 0.5 (usually nearly 1.0) times length of dorsal surface of labrum, opening rounded, not distinctly transverse, tormal arms thick (Fig. 19A). *Diabroctis, Sulcophanaeus, Phanaeus, Oxysternon.*

MANDIBLES AND MAXILLAE: These mouthparts are remarkably similar in all taxa studied; they yielded no taxonomic characters useful at the supraspecific level.

LABIUM: Unique variation of the labium is restricted to *Megatharsis buckleyi,* which, unlike any other phanaeine, has one-segmented labial palpi (Fig. 154); the dorsal surface of each segment bears a membranous slit (Fig. 155, arrow) possibly indicating an incomplete line of fusion. Other labial characters, with wider taxonomic application, include the following three:

11. SHAPE OF MENTUM:

a. weakly emarginate—anterior emargination shallow or scarcely distinct, its depth less than ¼ (with few exceptions ⅛ or less) greatest length of mentum; greatest width of mentum usually less than 1.5 (approaching 1.0 in *Dendropaemon*) times greatest length (Figs. 152-154, 156-157). *Coprophanaeus, Dendropaemon, Tetramereia, Homalotarsus, Megatharsis.*

b. strongly emarginate—anterior emargination deeper, depth at least ¼ (usually ⅓ or more) length of mentum; width of mentum almost always 1.5 or more times length (Figs. 25, 158). *Diabroctis, Sulcophanaeus, Phanaeus, Oxysternon.*

12. MEDIAN LOBE OF HYPOPHARYNX:

a. present—large, distinct lobe at summit of premental groove (Fig. 26, mlhpx). All genera except those mentioned below.

b. absent—no distinct lobe present. *Dendropaemon, Tetramereia, Homalotarsus* (inf), *Megatharsis.*

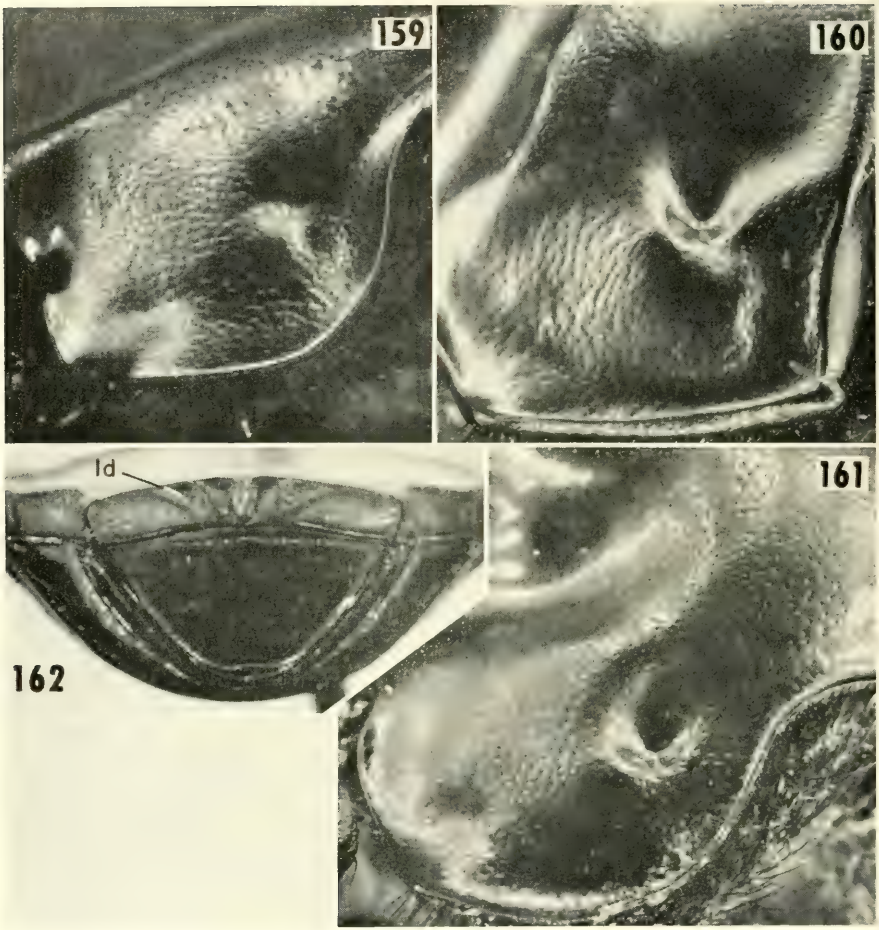
13. PREMENTAL SCLERITES:

a. completely sclerotized—entire sclerite darkly sclerotized (Fig. 30, pmts). *Phanaeus, Oxysternon.*

b. marginally sclerotized—only a C-shaped portion of posterior margin darkly sclerotized, otherwise weakly sclerotized (Figs. 150-151, pmts). All genera except *Phanaeus* and *Oxysternon.*

There exists another labial character—of great interest but little taxonomic value at the supraspecific level—concerning the position of the glossae, which varies between the following extremes:

a. appressed—glossae closely appressed along mesal margins for at least basal half of their lengths, completely closing over median groove of

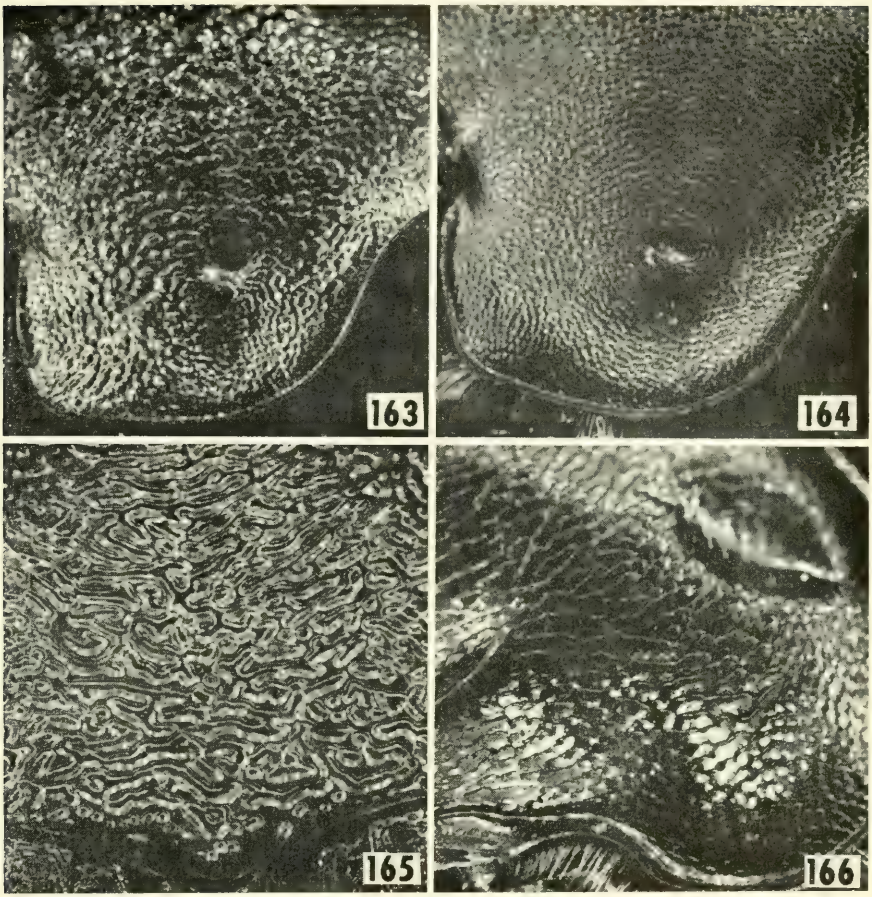


FIGS. **159-162. 159,** *Phanaeus pyrois,* male, left side of pronotum; **160,** *Oxysternon conspicillatum,* male, same; **161,** *Phanaeus haroldi,* female, same; **162,** *Dendropaemon viridis,* caudal view of pygidium.

prementum and enclosing between their bases median lobe of hypopharynx (if present) (Fig. 26).

b. separated—glossae widely separated basally, not touching mesally at any point; median groove of prementum exposed, median lobe of hypopharynx (if present) free (Fig. 149).

Species showing the above extremes and intermediate positions are included in each of the multispecific genera except *Oxysternon,* all examined species of which have appressed glossae. The following, for each genus, lists three common species showing, respectively, appressed, intermediate and separated glossae:



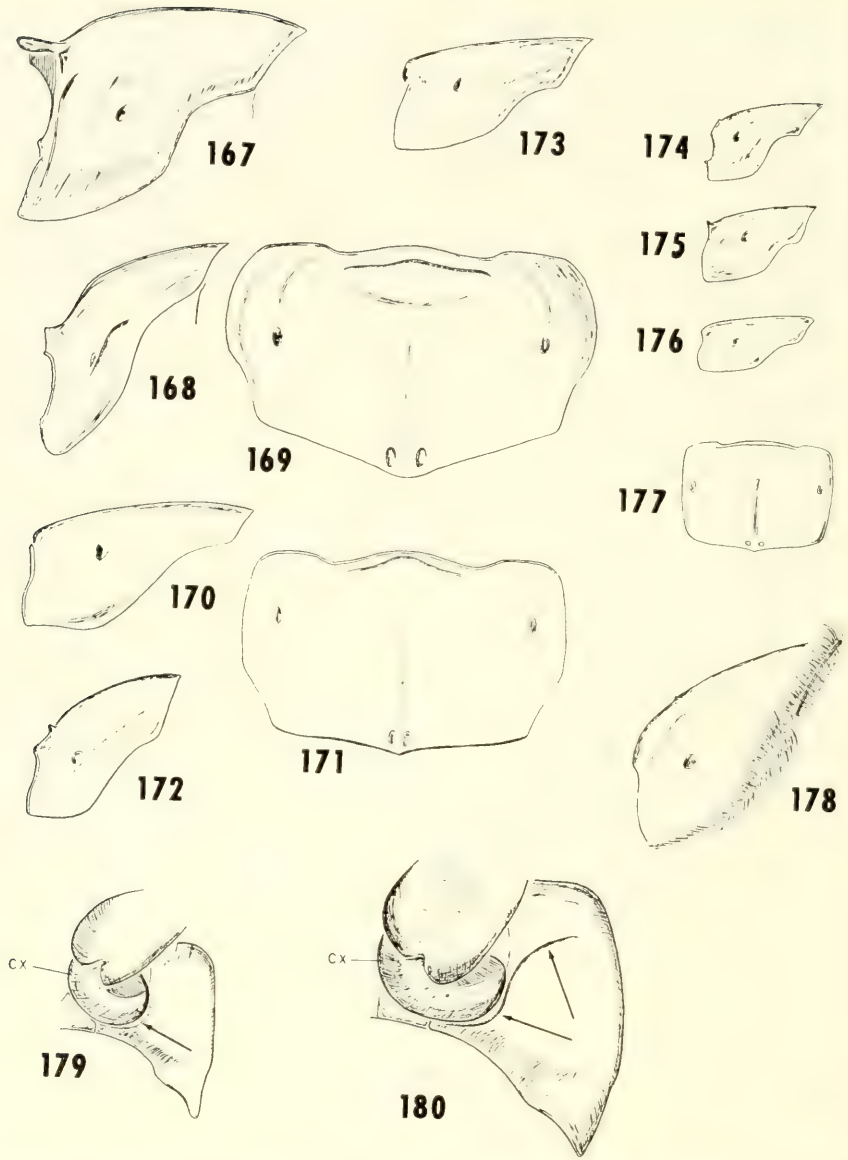
Figs. **163-166.** **163,** *Phanaeus damocles,* female, antero-lateral portion of pronotum; **164,** *P. triangularis,* female, same; **165,** *P. vindex,* female, postero-median portion of pronotum; **166,** *Coprophanaeus jasius,* female, left antero-lateral portion of pronotum.

Phanaeus: vindex, palaeno, quadridens
Sulcophanaeus: faunus, imperator, batesi
Coprophanaeus: ensifer, jasius, milon
Dendropaemon: viridipennis, denticollis, renatii

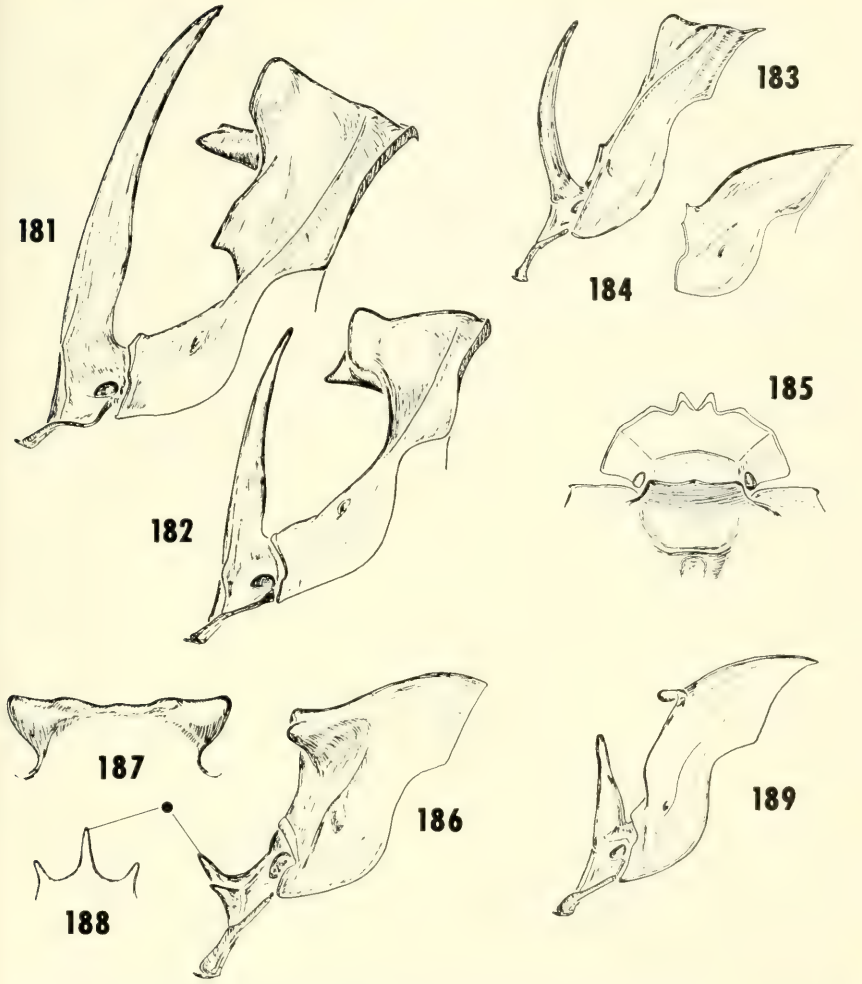
The glossae of *Megatharsis* are appressed; those of *Tetramereia* and *Homalotarsus* (inf) are of intermediate position.

Thoracic Segments

The shape of the pronotum of most phanaeines differs markedly between the sexes and among species. Like those of the head, pronotal outgrowths usually vary allometrically within single local populations. The form of the

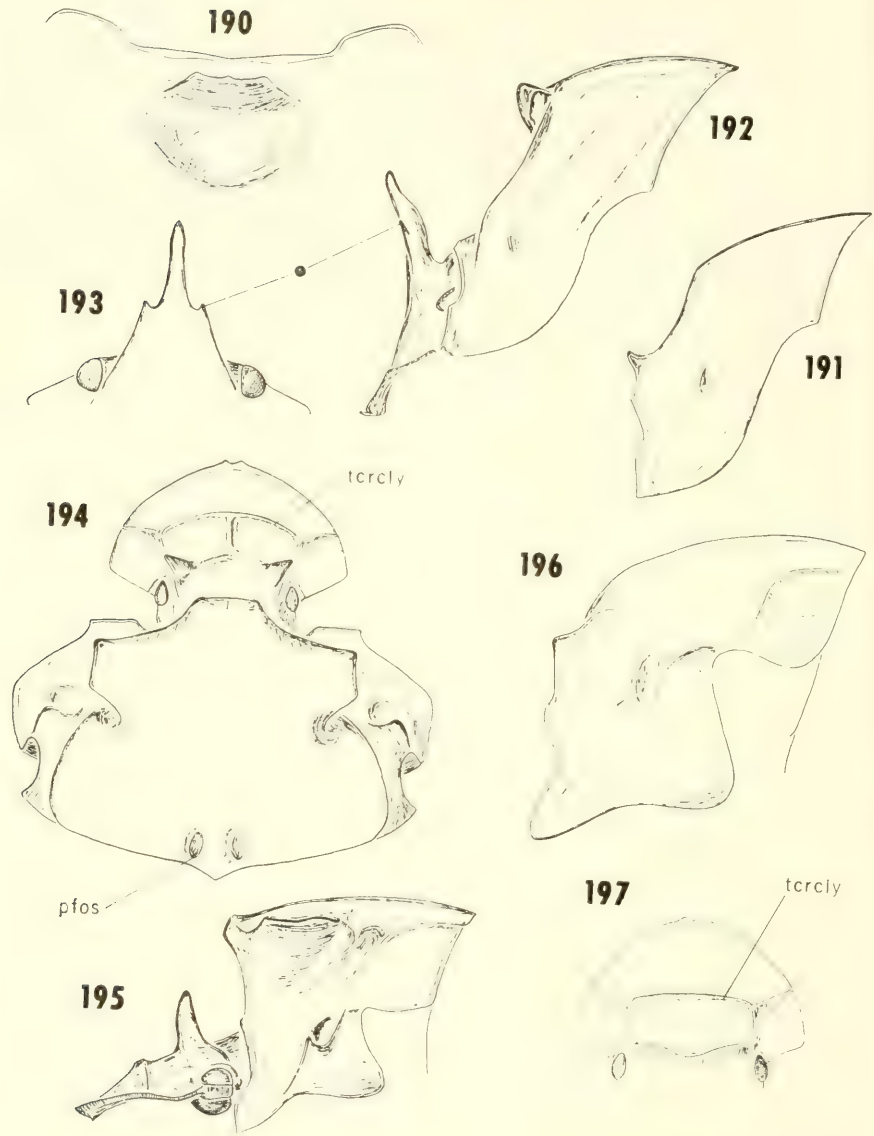


FIGS. **167-180.** **167,** *Dendropaemon amyntas,* male, lateral view of pronotum; **168,** *D. renatii,* female, same; **169,** same, dorsal view of pronotum; **170,** *D. viridis,* male, lateral view of pronotum; **171,** same, dorsal view of pronotum; **172,** *Tetramereia convexa,* lateral view of pronotum; **173,** *Dendropaemon fractipes,* same; **174,** *D. denticollis,* same; **175,** *D. haroldi,* same; **176,** *D. nitidicollis,* same; **177,** same, dorsal view of pronotum; **178,** *Megatharsis buckleyi,* lateral view of pronotum; **179,** *D. haroldi,* ventral view of left side of prothorax and base of leg; **180,** *D. viridipennis,,* same.

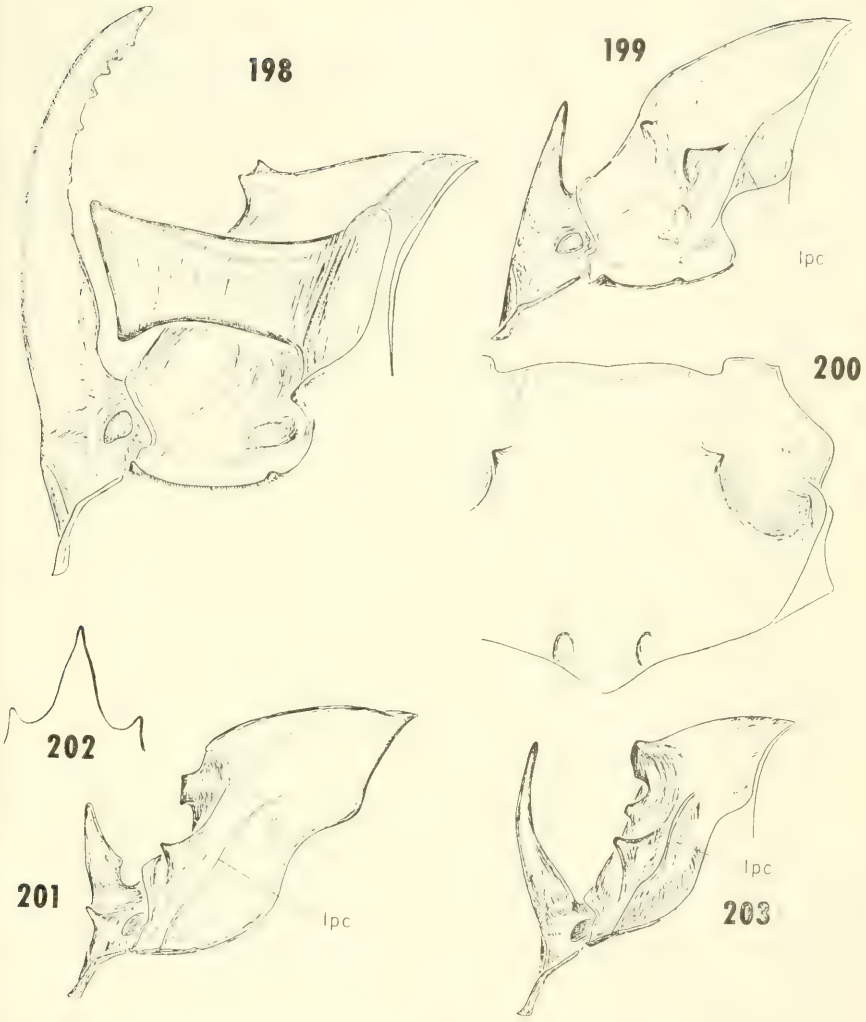


FIGS. **181-189.** **181,** *Coprophanaeus lancifer,* male, lateral view of head and pronotum; **182,** same, female; **183,** *C. saphirinus,* male, same; **184,** same, female, lateral view of pronotum; **185,** *C. pertyi,* female, dorsal view of head and anterior portion of prothorax; **186,** *C. pluto,* male, lateral view of head and pronotum; **187,** same, dorsal view of median pronotal prominence; **188,** same, anterior view of cephalic process; **189,** *C. pertyi,* male, lateral view of head and pronotum.

male pronotum varies greatest among species and is often distinctive of a species. Female pronotal form varies less among closely related species; indeed, the females of some groups of species (e.g., *Phanaeus daphnis* and related species) are impossible to distinguish using secondary sexual characters of the head and pronotum, even though the males may be quite distinct. It is difficult to arrange pronotal variation in shape into reasonably distinct



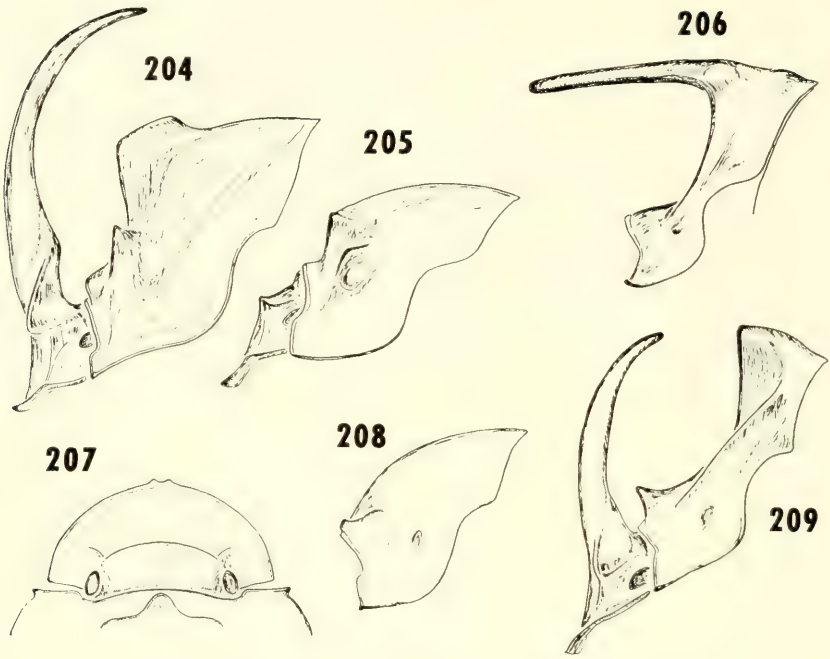
FIGS. 190-197. **190,** *Coprophanaeus jasius,* female, dorsal view of anterior portion of pronotum; **191,** same, lateral view of pronotum; **192,** same, male, lateral view of head and pronotum; **193,** same, male, anterior view of cephalic process; **194,** *Diabroctis mimas,* male, dorsal view of head and pronotum; **195,** same, lateral view; **196,** same, female, lateral view of pronotum; **197,** same, female, dorsal view of head.



FIGS. 198-203. 198, *Sulcophanaeus faunus,* male, lateral view of head and pronotum; 199, same, female; 200, same, female, dorsal view (incomplete) of pronotum; 201, *S. carnifex,* female, lateral view of head and pronotum; 202, same, female, anterior view of cephalic process; 203, same, male, lateral view of head and pronotum.

character states. Obvious types do exist, although their taxonomic reliability is reduced by a fairly high incidence of presumed convergence, particularly among males. In general, however, closely related species have similar pronotal shape.

Characters 14 and 15 treat pronotal types based on the shape and position of various projections, concavities, etc. Character 14 is based on well de-



FIGS. **204-209.** **204,** *Sulcophanaeus imperator,* male, lateral view of head and pronotum; **205,** same, female; **206,** *S. velutinus,* male, lateral view of pronotum; **207,** *S. chryseicollis,* female, dorsal view of head and anterior portion of pronotum; **208,** same, female, lateral view of pronotum; **209,** same, male, lateral view of head and pronotum.

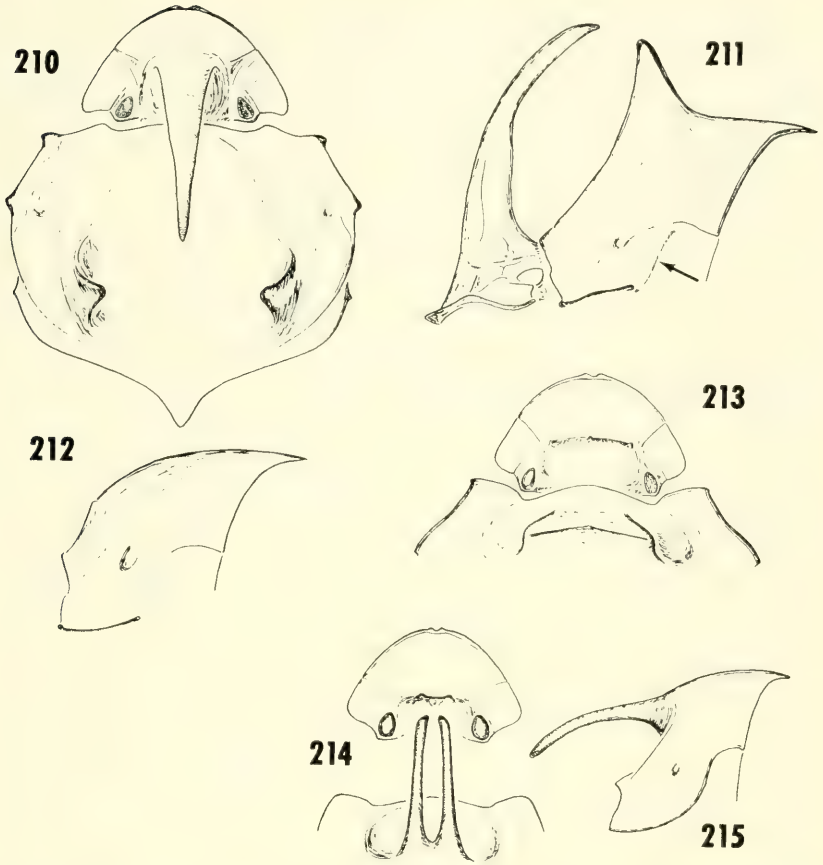
veloped ("major") individuals; less well developed males, while most often presenting reduced versions of the same features, may appear quite distinct. Like cephalic structure, variation in pronotal shape among conspecific females is much less pronounced than among males; thus, the types defined in character 15 should apply equally well to large and small individuals. The following do not include unique types; furthermore, since the variation within types is sometimes quite wide, the defined types should not be considered strictly mutually exclusive.

14. SHAPE OF PRONOTUM OF MALE:

a. type A—postero-lateral angles produced laterally as rounded lobes, giving pronotum a decidedly triangular or trapezoidal shape as seen dorsally; usually flattened dorsally, though sometimes convex or concave and bearing one or more tubercles or stronger prominences on dorsal surface (Figs. 35-36, 218-219, 223-226, 228).

b. type B—bearing two latero-median processes separated by concavity (Figs. 210-211, 216-217).

c. type C—strongly and widely raised antero-medially, bearing trans-



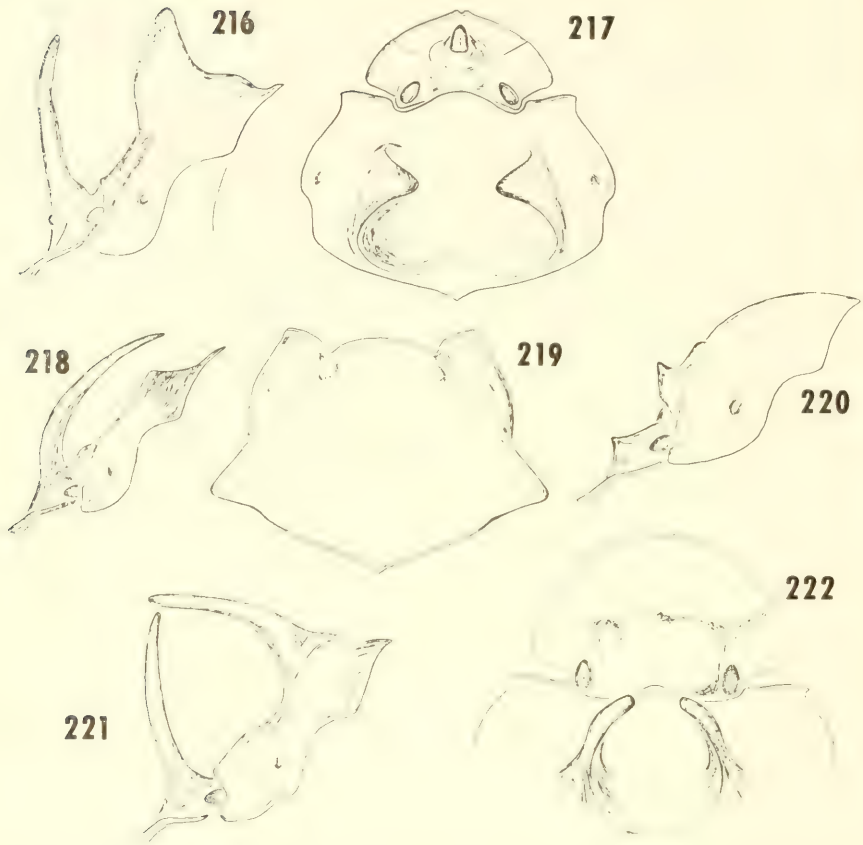
FIGS. 210-215. **210,** *Oxysternon conspicillatum,* male, dorsal view of head and pronotum; **211,** same, lateral view; **212,** same, female, lateral view of pronotum; **213,** same, dorsal view of head and anterior portion of pronotum; **214,** *O. curvispinum,* male, dorsal view of head and anterior portion of pronotum (separated); **215,** same, lateral view of pronotum.

verse angulate prominence or carina, anterior to which pronotal surface is vertical or concave (Figs. 167, 186, 189, 192, 194-195).

d. type D—bearing four tubercles or prominences in transverse row near posterior margin of pronotum; tubercles may differ little in size or inner two or outer two may be strong projections (Figs. 198, 203-204).

e. type E—pronotum deeply and widely concave medially, posterior margin of concavity bearing massive, saddle-shaped prominence (Fig. 181).

f. type F—flattened and sloping anteriorly with pair of closely set postero-median prominences which may be crest-like or elongate projections (Figs. 183, 206, 209).



FIGS. 216-222. **216,** *Phanaeus dejeani,* male, lateral view of head and pronotum; **217,** same, dorsal view; **218,** *P. endymion,* male, lateral view of head and pronotum; **219,** same, male, dorsal view of pronotum; **220,** same, female, lateral view of head and pronotum; **221,** *P. haroldi,* male, same; **222,** same, female, dorsal view of head and anterior portion of pronotum.

15. SHAPE OF PRONOTUM OF FEMALE:

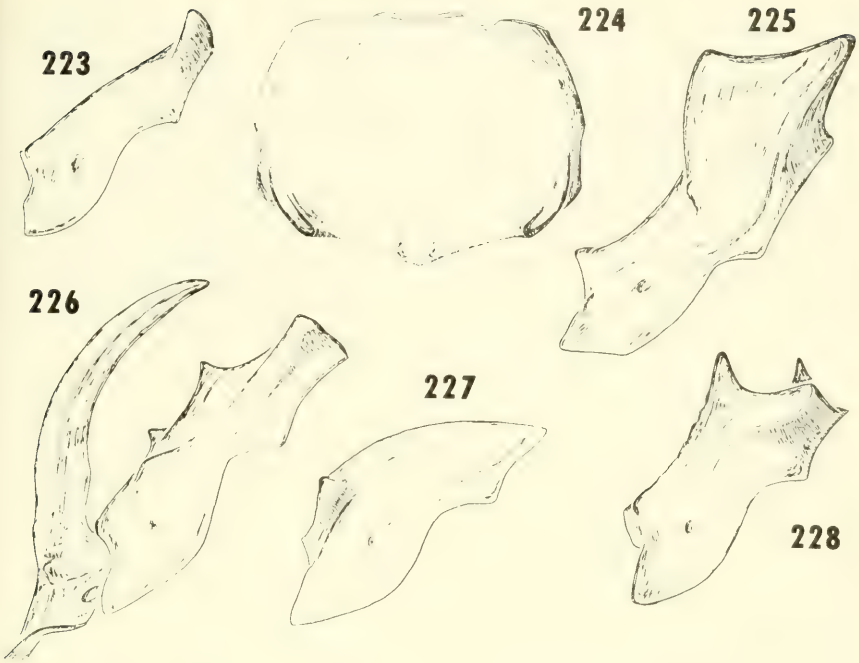
a. type A—convex except for antero-median concavity bordered anteriorly by transverse carina or crest (Figs. 184-185, 190-191).

b. type B—convex except for three closely set antero-median tubercles, median one of which may be dentate (Fig. 220).

c. type C—convex except for low, antero-median prominence bordered anteriorly by unevenly bowed carina (Figs. 207-208).

d. type D—convex but bearing an antero-median transverse carina or wide ridge anterior to which pronotal surface sometimes nearly vertical (Figs. 37-38, 196, 205, 213, 227).

e. type E—evenly convex (Figs. 178, 310-315).



Figs. 223-228. 223, *Phanaeus lugens,* male, lateral view of pronotum; 224, same, dorsal view; 225, *P. demon,* male, lateral view of pronotum; 226, *P. mexicanus,* male, lateral view of head and pronotum; 227, same, female, lateral view of pronotum; 228, *P. daphnis,* male, lateral view of pronotum.

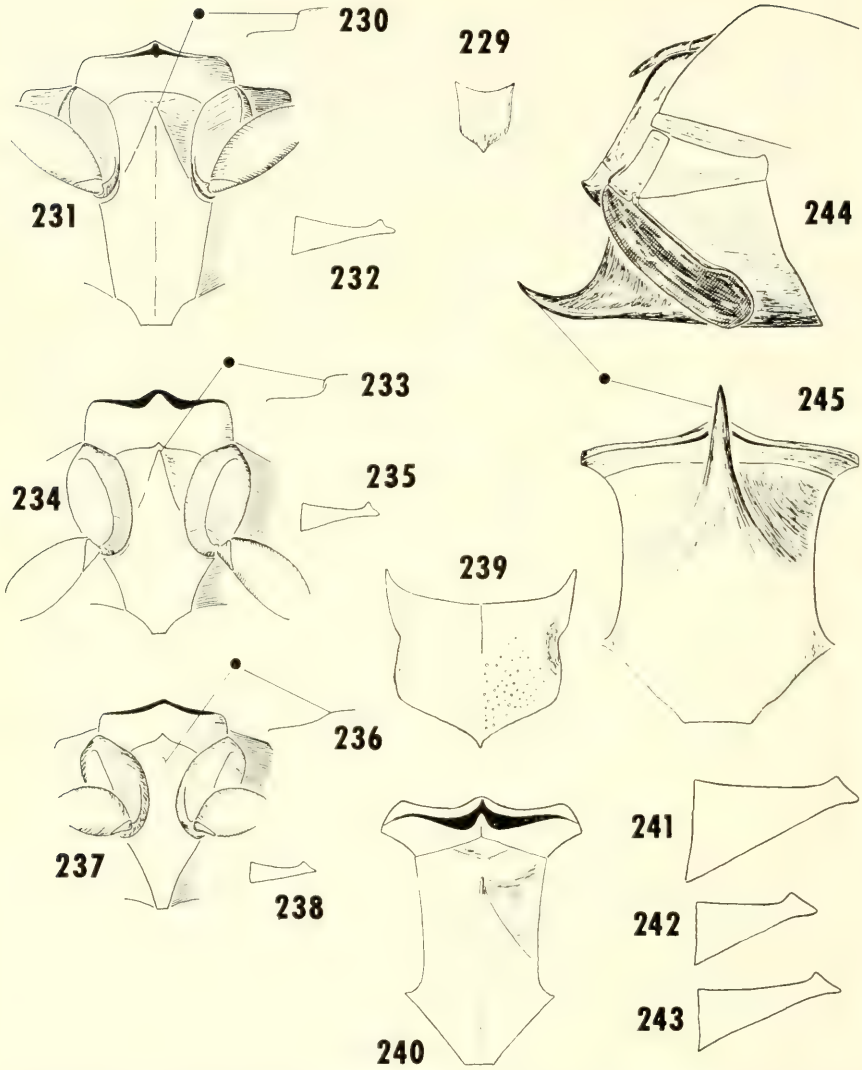
16. pronotal sculpturing: The texture of the pronotal surface varies considerably. Although intermediate conditions occur in some species most supraspecific taxa are characterized by one of the following states:

a. smooth-punctate—completely smooth or with limited weakly roughened areas, but entire surface punctate (Figs. 159-161).

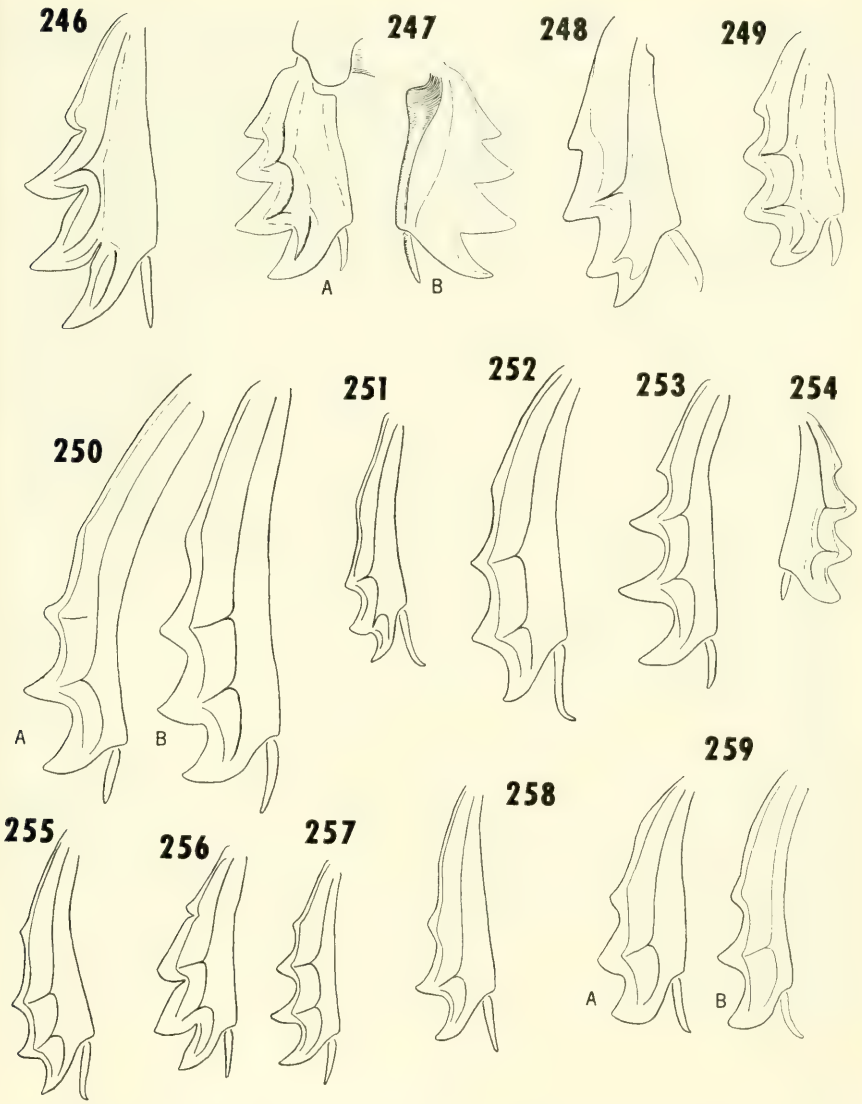
b. roughened—surface entirely granulate (Fig. 164), granulo-rugose (Fig. 163) or rugose (Fig. 165); if distinct puncturing present, usually restricted to postero-median area. In most *Coprophanaeus* and *Coprophanaeoides* the roughening, at least anteriorly, is in the form of transverse ridging (Fig. 166).

The following are other taxonomically restricted variations of the prothorax:

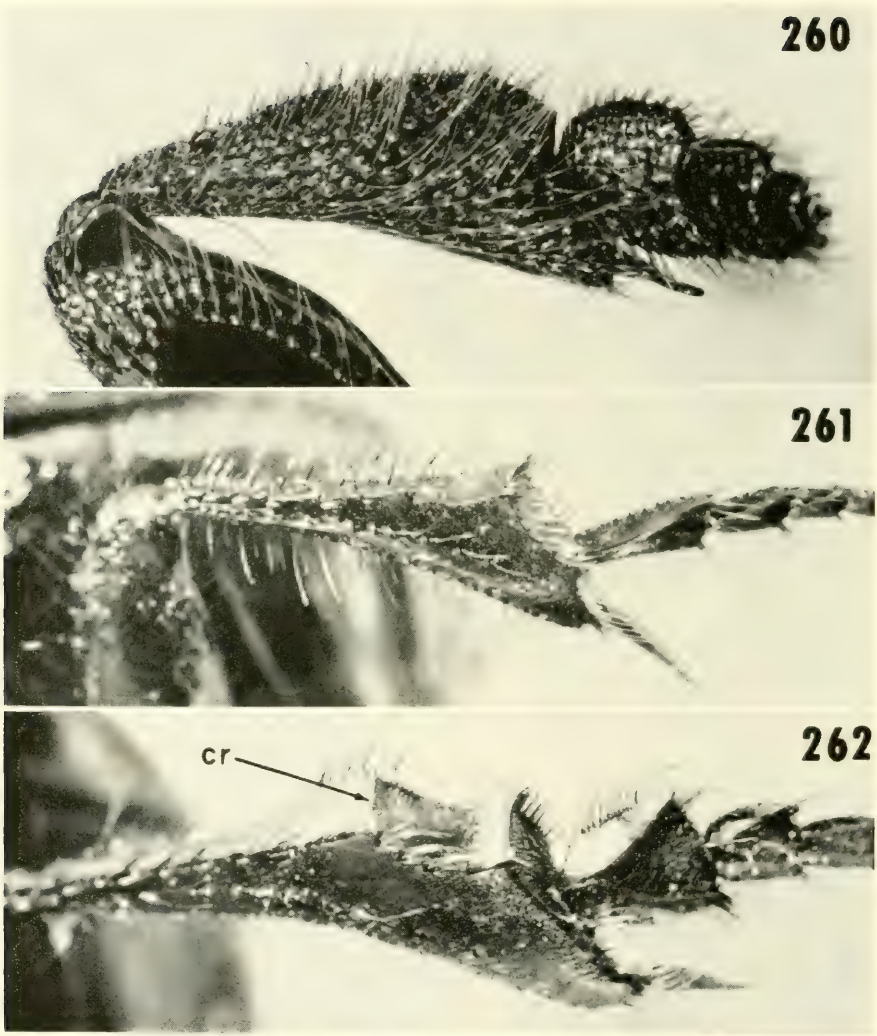
posterior pronotal fossae: These fossae are usually evident as puntiform pits or large rounded depressions on the postero-medial angle of the pronotum (Fig. 194, pfos); they are characteristically absent only in *Oxysternon,* the postero-median angle of the pronotum of which is a strongly produced, acute process fitting between the bases of the elytra (Fig. 210).



FIGS. 229-245. **229,** *Dendropaemon denticollis,* dorsal view of mesoscutellum; **230,** same, lateral view of antero-median angle of metasternum; **231,** same, ventral view of pterothorax; **232,** same, lateral view of metepisternum; **233,** *D. haroldi,* same as 230; **234,** same, same as 231; **235,** same, same as 232; **236,** *D. nitidicollis,* same as 230; **237,** same, same as 231; **238,** same, same as 232; **239,** *Homalotarsus impressus,* dorsal view of mesoscutellum; **240,** same, ventral view of mesosternum and median area of metasternum; **241,** *Dendropaemon renatii,* lateral view of metepisternum; **242,** *D. bahianus?,* same; **243,** *D. hirticollis,* same; **244,** *Oxysternon conspicillatum,* lateral view of pterothorax (elytra in place, coxae removed); **245,** same, ventral view of mesosternum and median area of metasternum.

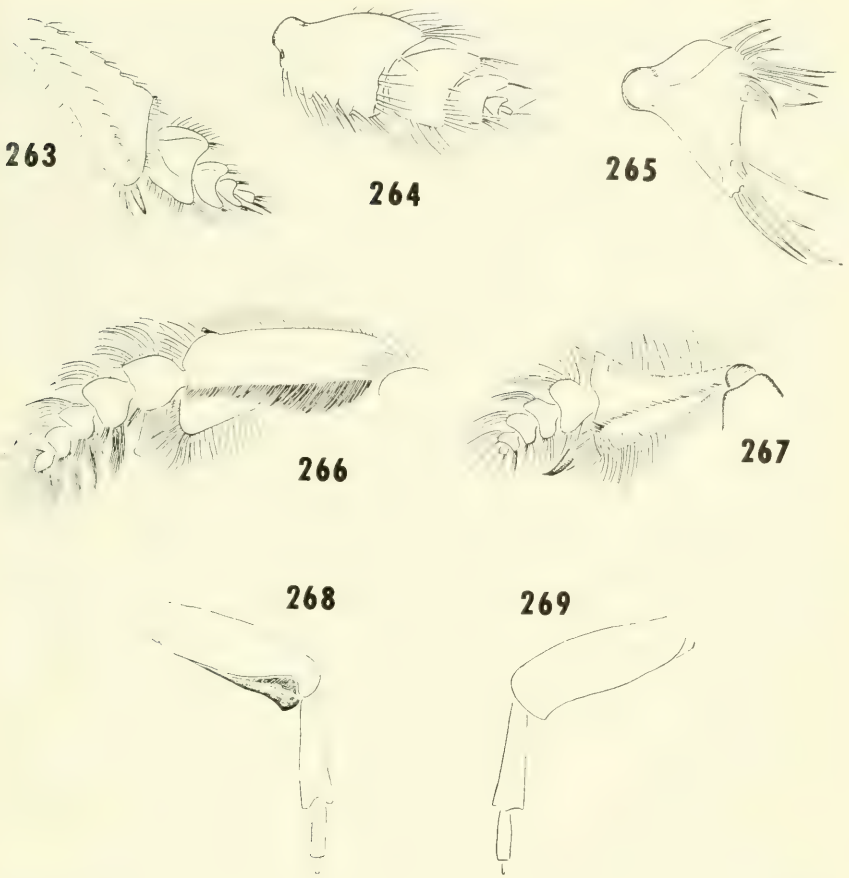


FIGS. **246-259.** Front tibiae. (All Figs. except 247B are of anterior surfaces.) **246,** *Coprophanaeus jasius;* **247,** *Dendropaemon viridis* (A—anterior surface, B—posterior surface); **248,** *Megatharsis buckleyi;* **249,** *Tetramereia convexa;* **250,** *Diabroctis mimas* (A—male, B—female); **251,** *Sulcophanaeus noctis,* male; **252,** *S. columbi,* female; **253,** *S. imperator,* male; **254,** *Homalotarsus impressus;* **255,** *Phanaeus haroldi,* female; **256,** *P. blanchardi,* female; **257,** *P. kirbyi,* male; **258,** *Oxysternon festivum,* male; **259,** *Phanaeus mexicanus* (A—female, B—male).



FIGS. **260-262. 260,** *Homalotarsus impressus,* female, dorsal view of apex of femur, tibia and tarsus of right hind leg; **261,** *Phanaeus vindex,* male, ventro-lateral view of left hind tibia and tarsus; **262,** *Sulcophanaeus faunus,* male, same.

LATERAL PRONOTAL CARINAE: These carinae (Figs. 199, 201, lpc) are distinct only in the *Sulcophanaeus faunus* group. In other *Sulcophanaeus,* in *Megaphanaeus* and *Diabroctis* (particularly males) the pronotum is thickened along a non-carinate line in the same relative position as this carina. The lateral pronotal carinae of *S. columbi* are produced postero-laterally as small crests. These angles produce a pronotal shape similar to type A (char-

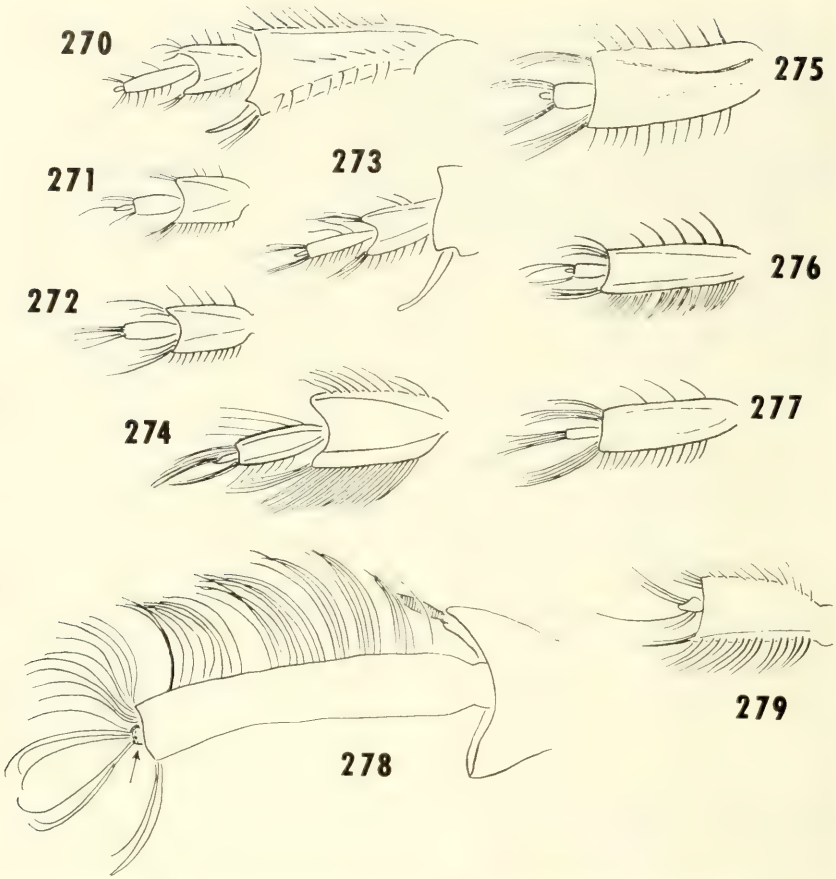


FIGS. 263-269. **263,** *Tetramereia convexa,* ventral view of left hind tibia and tarsus; **264,** *Homalotarsus impressus,* dorsal view of right hind tarsus; **265,** same, ventral view of first segment of right mesotarsus; **266,** *Megatharsis buckleyi,* dorsal view of left hind tibia and tarsus; **267,** same, dorsal view of middle left tibia and tarsus; **268,** *Dendropaemon viridis,* dorsal view of right hind leg (except tarsus); **269,** same, ventral view.

acter 14), suggesting that the rounded postero-lateral lobes characteristic of type A are homologs of lateral pronotal carinae.

TRANSVERSE PROPLEURAL CARINAE: These carinae are present only in *Dendropaemon, sen. str.* When complete, each extends along the posterior margin of the procoxal cavity onto the propleural surface lateral to the coxa (Fig. 180, arrows); when incomplete, each is restricted along the posterior margin of the coxal cavity (Fig. 179, arrow).

Variation in the pterothoracic segments of taxonomic significance is limited to the spinate prolongation of the metasternum of *Oxysternon* (Figs.



FIGS. **270-279. 270,** *Dendropaemon denticollis,* ventral view of right hind tibia and tarsus; **271,** *D. haroldi,* ventral view of right hind tarsus; **272,** *D. smaragdinum,* same; **273,** *D. lobatum*?, same; **274,** *D. renatii,* same; **275,** *D. amyntas,* same (worn); **276,** *D. viridipennis,* same; **277,** *D. viridis,* same; **278,** *D. ganglbaueri,* same (arrow points to small second segment); **279,** same, ventral view of left middle tarsus.

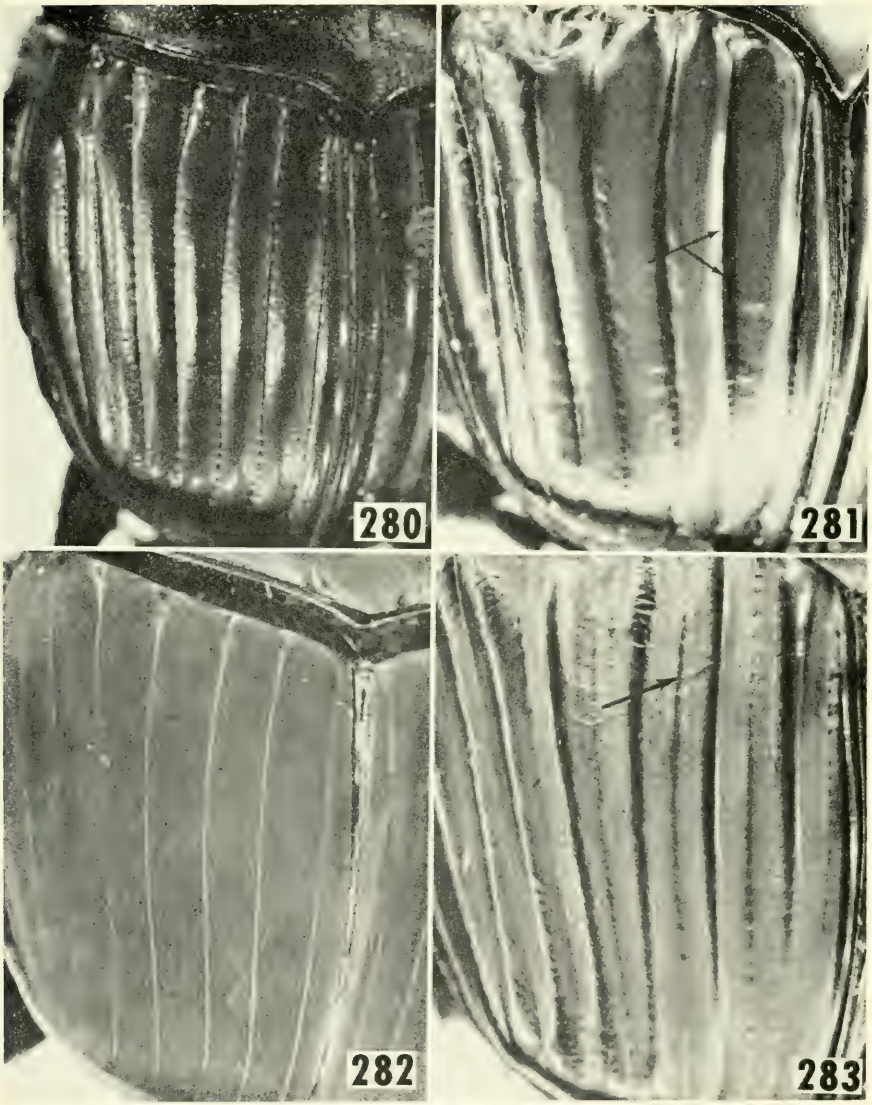
244-245) and to various aspects of body shape variation in *Dendropaemon* (Figs. 229-238, 241-243), which are discussed more fully in the systematic section.

LEGS

17. FRONT TARSI OF FEMALE:

a. present—short, five-segmented tarsi inserted on inner apical angle of tibia. *Diabroctis, Sulcophanaeus* (ex), *Oxysternon, Phanaeus, Megaphanaeus.*

b. absent—*Coprophanaeus, sen. str., Metallophanaeus, Dendropaemon, Tetramereia, Homalotarsus, Megatharsis.*

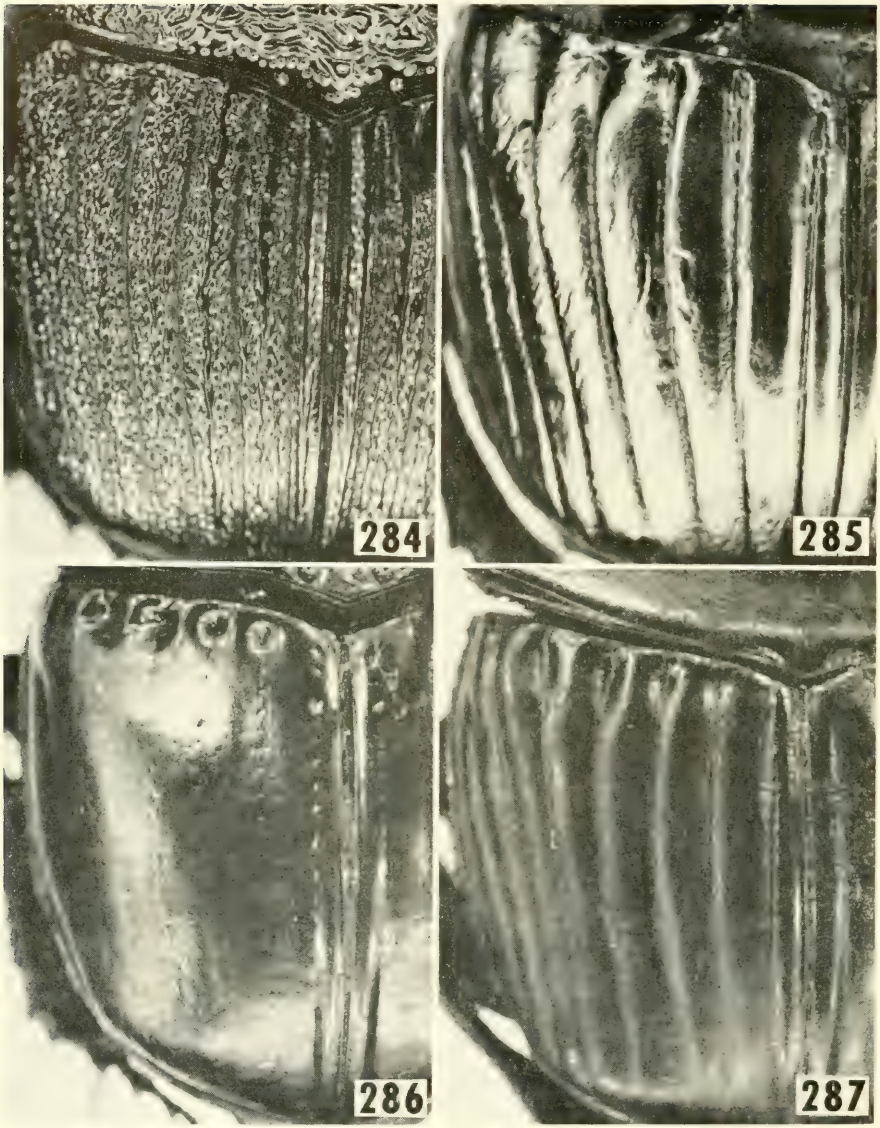


FIGS. **280-283.** Left elytron, dorsal views. **280,** *Oxysternon (M.) curvispinum;* **281,** *O. conspicillatum* (arrows point to second stria); **282,** *Sulcophanaeus noctis;* **283,** *S. columbi* (arrow points to third stria).

18. FRONT TIBIAE:

a. *Coprophanaeus*-type—very strongly and acutely quadridentate, teeth separated basally by very narrow spaces; apical three teeth always carinate (Fig. 246). *Coprophanaeus.*

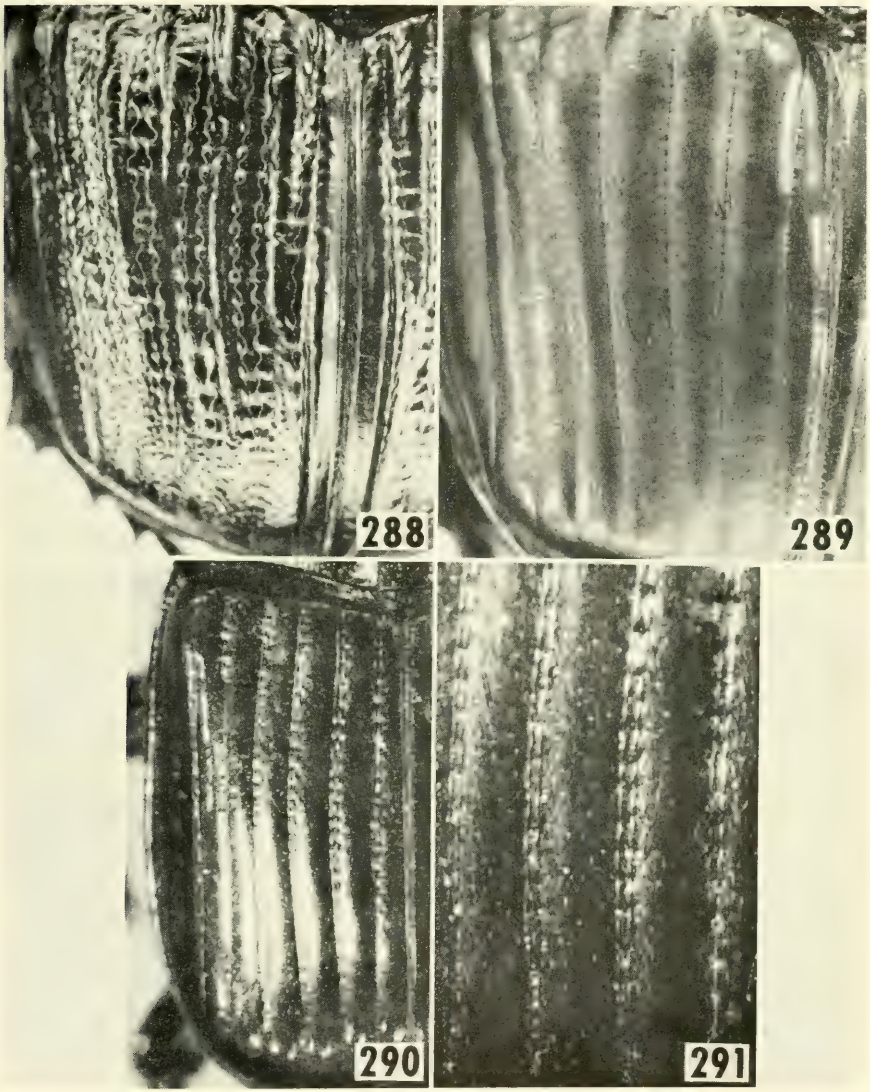
b. *Dendropaemon*-type—acutely quadridentate, teeth not separated



FIGS. 284-287. Left elytron, dorsal views. 284, *Phanaeus vindex;* 285, *P. mexicanus;* 286, *P. damocles;* 287, *P. endymion.*

by narrow spaces basally; apical three teeth always carinate; inner basal angle expanded, covering apex of femur (Fig. 247). *Dendropaemon* (except *ganglbaueri*).

c. *Phanaeus*-type—tridentate or quadridentate, teeth acute or rounded, separated basally by wide, usually rounded spaces; apical two or three teeth

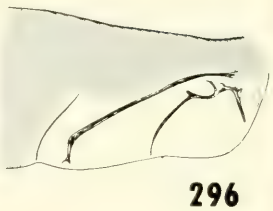


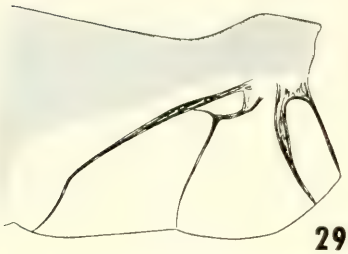
Figs. **288-291.** Left elytron, dorsal views. **288,** *Coprophanaeus lancifer;* **289,** *C. jasius;* **290,** *Dendropaemon viridis;* **291,** same (higher magnification to show carinulate striae).

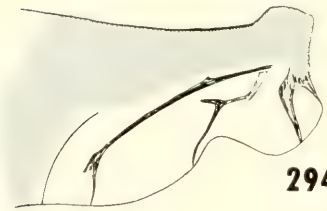
carinate (Figs. 248-259); tibiae of male sometimes distinctly narrower than those of female (Figs. 250, 259). All genera except above two.

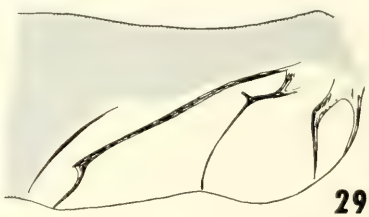
19. MIDDLE AND HIND TARSI:

a. two-segmented—some *Dendropaemon, sen. str., Paradendropaemon* (Figs. 272, 277-279).







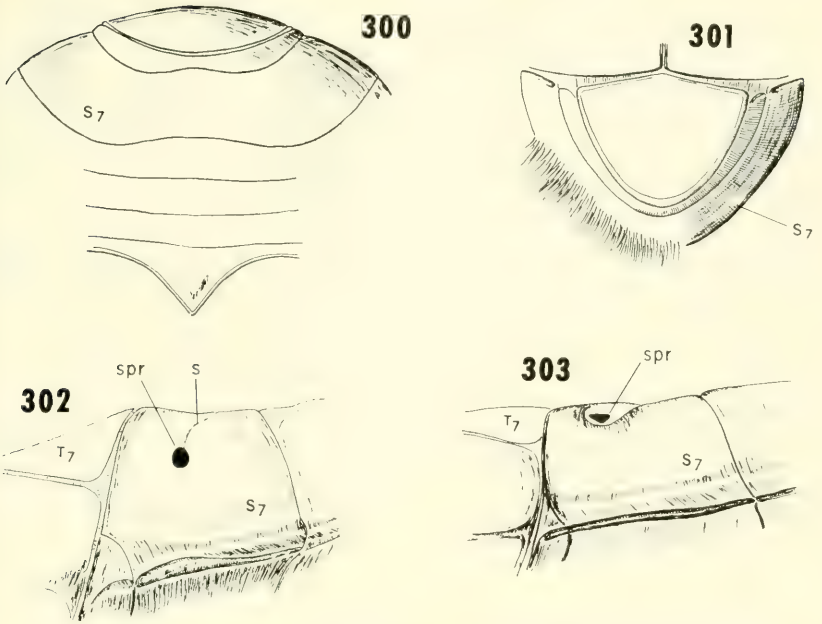


FIGS. **292-299.** (Stippling indicates areas for which detail not shown.) **292,** *Coprophanaeus jasius,* right hind wing; **293,** *Sulcophanaeus chryseicollis,* base of left hind wing; **294,** *Dendropaemon renatii,* same; **295,** *D. piceum,* same; **296,** *Megatharsis buckleyi,* same; **297,** *Tetramereia convexa,* same; **298,** *Dendropaemon haroldi,* same; **299,** *D. amyntas,* same.

b. three-segmented—some *Dendropaemon, sen. str., Coprophanaeoides* (Figs. 270-271, 273-276).

c. four-segmented—*Tetramereia* (Fig. 263).

d. five-segmented—all other genera; relative shapes and sizes of segments usually as in *vindex* (Fig. 64); shapes of tarsal segments of *Megatharsis* (Figs. 266-267) and *Homalotarsus* (Figs. 264-265) unique.



FIGS. **300-303.** **300,** *Dendropaemon ganglbaueri,* female, ventral view of abdomen; **301,** *Megatharsis buckleyi,* female, caudal view of abdomen (setae shown on left side only); **302,** *Sulcophanaeus carnifex,* lateral view of right dorso-lateral extremity of abdominal sternum 7 and adjacent areas; **303,** *Coprophanaeus dardanus,* same.

TRANSVERSE TIBIAL CARINA: In addition to a few isolated species (e.g., *Sulcophanaeus imperator*), this carina (Fig. 262, cr) is restricted to the *Sulcophanaeus faunus* group, *Diabroctis,* and the *Oxysternon festivum* group.

Other variation of the legs includes the following, relatively isolated specializations: The setigerous granulation of the dorsal surface of the hind legs of *Homalotarsus* (Fig. 260) and the characteristic expansion of the lower apical angle of the middle and hind femora of *Dendropaemon* (Figs. 268-269).

WINGS

20. SCULPTURING OF ELYTRAL INTERSTRIAE:

a. smooth—no distinctly punctured or rugose areas; if punctures present, restricted to minute punctures clearly visible only with high (20×) magnification (Figs. 281-282, 285, 287, 289).

b. punctate—distinctly punctured, punctures visible with low (10×) or no magnification (Figs. 280, 286, 290).

c. rugose—granulate, rugose or very heavily punctured with coalescing of punctures (Figs. 284, 288).

21. RELIEF OF ELYTRAL INTERSTRIAE:

a. flat—(Figs. 282, 284, 286).

b. convex—usually evenly (Figs. 280-281, 285, 287, 290-291) but sometimes raised only medio-longitudinally such that striae appear to lie in broad, shallow troughs (Fig. 283).

22. STRIAE:

a. carinulate—bordered laterally by fine carinae which may be straight (Figs. 290-291) or undulate (Fig. 288). *Megaphanaeus, Dendropaemon* (except *ganglbaueri*) and isolated instances in other genera.

b. simple—distinct or very weak, sometimes punctate lines with undefined lateral margins (Figs. 280-287, 289). All taxa except above.

Of the characters of the *hind wing* only one is reasonably consistent at the supraspecific level: a distinct notching of the wing between the vannal and jugal lobes (Figs. 292, 294-295, 298) characteristic of *Coprophanaeus, sen. str., Coprophanaeoides* and some *Dendropaemon, sen. str.;* all others (except *Phanaeus bispinus*) have no emargination (Figs. 71, 293, 296, 299).

ABDOMEN

Only the following features comprise marked departure from the otherwise striking consistency in abdominal structure among the phanaeines studied:

POSITION OF LAST (7TH) ABDOMINAL SPIRACLE: The opening of this spiracle assumes three positions.

a. marginal—spiracular opening located in membrane connecting tergum 7 and sternum 7 (Fig. 72, spr_7); usually visible only dorsally; this is the most common position.

b. intermediate—located in a notch in dorsal margin of sternum 7; usually visible laterally (Fig. 303).

c. intrasternal—located within dorso-lateral portion of sternum 7 (Fig. 302, spr), faint suture (s) extending from spiracle to dorsal margin of sternum 7; visible only dorsally.

Supposedly the evolution of position of this spiracle has included its ventral migration and/or dorsal extension of sternum 7, ultimately becoming isolated by closure of the sternum along a distinct suture. The intrasternal position is the least frequent and characteristic only of *Megaphanaeus* and *Mioxysternon* as well as isolated species-pairs in *Sulcophanaeus.* States a. and b. occur in a random taxonomic pattern.

The only other noteworthy abdominal variations are the lateral depressions of the base of the pygidium of *Dendropaemon* (Fig. 162, ld), the sternal fringes of *Megatharsis* (Fig. 301) and the abnormally elongate sternum 7 of *Paradendropaemon* (Fig. 300, s_7).

PART IV: ADAPTIVE SIGNIFICANCE OF ASPECTS OF PHANAEINE SKELETAL MORPHOLOGY

What is known about the habits of phanaeines, as well as other Scarabaeinae, has been well summarized by Halffter and Matthews (1966). One important group of adaptive modifications of dung beetles, those related to coprophagy, has been discussed by them (pp. 241-248). As they and others have pointed out, adult scarabaeines are basically fossorial animals. Although they seek food on the surface, a large part of the feeding, mating and reproductive activities is carried on in underground tunnels and chambers excavated by the beetles. Efficient fossorial habit requires a highly specialized morphology. The purpose of this discussion is to bring out certain aspects of adult scarabaeine morphology, as illustrated specifically by the phanaeines, presumably related to digging habits. Certain characters here deemed fossorial are no doubt also important in other behavioral contexts; indeed, a portion of this discussion is the examination of just such a case. Nevertheless, it is assumed that the initial selective factors involved in their evolution from antecedent types favored morphological complements of fossorial behavior.

The fossorial features of phanaeines, and dung beetles in general, fall into two general categories: (1) structural modifications of direct use as digging tools, and (2) strengthening devices for increased body resistance to the generally compressive forces exerted on the body during digging and manipulation of soil (and food). Most of the features to be mentioned are shared with other Scarabaeinae and some other laparostict scarabaeids.

Structural Tools

The primary earth-moving structures are the head and front legs. The following modifications of the head capsule and legs of phanaeines presumably contribute to the efficiency of these organs as digging tools:

a. Differential expansion and ventral folding of the head sclerites—This trend has two very important adaptive consequences, (1) increase in the digging surface area of the head, principally through dorsal expansion of the clypeus, and (2) elimination of dorsal and lateral exposure of the head appendages, which are thereby protected from potential injury.

b. Clypeal dentition and transverse ridging—While the dorsum of the head (clypeus) is primarily employed in pushing and packing soil (and food), its anterior margin functions primarily as a scraper. Clypeal teeth and other irregularities produce sharper, thus more effective cutting instruments. In addition to teeth, the transverse ridging of the dorsal surface contributes to its overall abrasiveness.

c. Antero-lateral flattening and lateral toothing of the front tibiae—The front tibiae are principally scraping structures whose effectiveness is increased by dentate cutting edges.

d. Elongation, double articulation and transverse orientation of the front coxae—Elongation has effectively increased the surface area of the coxal margin available for muscle insertion. If increased musculation is to function efficiently to rotate the coxa, the axis of rotation of a subcylindrical coxa must be fixed by two articulations, one at each end. Transverse orientation of the coxa preserves an antero-posterior movement of the distal portion of the leg effective both for walking and digging movements (dirt is pushed *under* body).

e. Strong development and musculation of middle and hind legs—These legs, while not directly involved in digging, propel the body forward and, to a large extent, determine the effectiveness of digging movements of the head; they are strongly musculated. The tarsi are articulated so that, during propulsion of the body by middle and hind legs, they project laterally to allow firm implantation of the expanded distal ends of the tibiae.

STRENGTHENING DEVICES

To effectively aid digging movements, the body wall must provide rigid mechanical support. The following features (in addition to thickly sclerotized integument) presumably contribute to the overall body resistance necessary to withstand the stresses imposed by digging:

a. Cephalic brachium—While the brachium no doubt imparts necessary rigidity to the dorsal mandibular articulation, it also increases the resistance of the head capsule to compressive forces exerted on the expanded anterior portion of the head dorsum.

b. Complete division of the eye—The firm contact (along the postocular line) of the paraocular and postocular lobes of the parietals apparently relieves the eye from pressure transferred posteriorly from the head dorsum and from antagonistic pressure transferred anteriorly by resistance of the prothorax.

c. Intersegmental inflection of the body wall—Longitudinal compressive forces are borne by opposed inflected surfaces which distribute resistant forces over much greater areas than would be afforded by the mere opposing edges of sclerites. The most extensive inflections occur between the head and prothorax and between the prothorax and pterothorax. The narrowed posterior portion of the head capsule fits snugly against the prothorax in a receptacle formed by the inflection of the anterior prothoracic margin. Maintenance of this head-prothorax connection is enhanced in *Phanaeus* by the interlock mechanism formed by the postocular lobes of the parietals and emarginations in the anterior portion of the circumnotal ridge. The inflected posterior margin of the prothorax is opposed dorsally by anterior inflections of the elytra and mesepimera and ventrally by the antero-median prominence of the metasternum.

d. Rigidity of posterior part of body—Overall strengthening is achieved

by two complementary devices, firm interlocking and anchoring of the elytra and fusion of the abdominal sterna. Elytral interlocking is by means of an opposing ridge-groove mechanism along the elytral suture; anchoring of the elytra is affected by the metepisternal tabs, which maintain close elytral appression along the elytral suture by restricting lateral slippage of the elytra.

Concealment of all spiracles is apparently another important fossorial adaption. The thoracic spiracles are hidden by the overlap of the mesothorax by the prothorax; the abdominal spiracles are covered by the elytra. Directly exposed spiracles would no doubt be highly susceptible to obstruction by soil particles.

Secondary Modification of Fossorial Features

As mentioned above, certain basically fossorial characters have equally important adaptive significance in other behavioral contexts, such as feeding habit. *Coprophanaeus* is apparently exclusively a necrophagous genus while most other phanaeine genera are known to be principally coprophagous. In the context of necrophagy, the strong development of clypeal and front tibial dentition in *Coprophanaeus* is especially noteworthy. While dentition in the present sense is basically a fossorial adaptation, its degree of development in phanaeines is closely related to feeding habit. Strongly developed dentition in *Coprophanaeus* is probably directly related to the principal food of the genus, carrion. The resiliency of flesh is obviously much greater than that of dung. Hence, structural tools facilitating its collection would presumably be selectively advantageous for a necrophagous beetle. I have observed *Megaphanaeus* in Brazil using the foretibiae, employed with unmistakable cutting-slicing motions, and clypeus to shear flesh from animal carcasses, in the manner suggested by Halffter and Matthews (1966: 93). That *Coprophanaeus* is efficient at removing carcasses is well evidenced by the observation of Martínez (1959) that four individuals of *Coprophanaeus (Megaphanaeus) ensifer* cut into pieces and buried a 20 kg (44 lb) dog carcass in one night! I observed a somewhat lesser feat performed by five *C. (C.) jasius,* which disposed of an armadillo weighing approximately 2 kg in a similar period of time.

PART V: CLASSIFICATION OF THE PHANAEINES

That the phanaeine genera form a quite cohesive, natural assemblage has been assumed for many years. Early authors referring new taxa to the "Phanaei," "group of *Phanaeus*," etc., recognized the group primarily by the form of the antennal lamellae and lack of tarsal claws. These same features were stressed by MacLeay (1819) in proposing *Phanaeus* for certain Linnean species of *Scarabaeus*.

The first formal taxonomic recognition of a phanaeine assemblage was

Kolbe's "unterfam. Phanaeinae" (1905: 550), which included *Phanaeus, Gromphas, Bolbites, Oruscatus, Megatharsis* and *Dendropoemon* (sic). Kolbe apparently overlooked *Oxysternon* and *Diabroctis,* both of which were proposed for species of *Phanaeus* long before 1905. Gillet's checklist (1911) included the aforementioned genera (except *Diabroctis*) along with *Ennearabdus* and *Pteronyx* in Phanaeides, one of three subdivisions (though not called subtribes by him) of Coprini. Olsoufieff (1924) also applied the name Phanaeides to essentially the same assemblage as Gillet except that he included *Diabroctis* (as *Taurocopris*) and *Tetramereia* (as *Boucomontius*) and excluded (p. 16) both *Pteronyx* and *Ennearabdus.* The latter genus has since been placed in a tribe of its own, Ennearabdini (Pereira and Martínez, 1956). Moreover, Olsoufieff divided *Phanaeus* into five subgenera, *Sulcophanaeus, Coprophanaeus, Metallophanaeus, Megaphanaeus* and *Phanaeus, sen. str.* Blackwelder's checklist (1944) follows Olsoufieff except that the above subgenera are each raised to generic rank and *Pteronyx* and *Ennearabdus* are readmitted to Phanaeides.

Most modern workers have adopted a classification of Scarabaeinae based upon the keys given by Janssens (1946, 1949), in which the larger tribes are subdivided into subtribes. Accordingly, the phanaeine genera comprise Phanaeina, one of the three subtribes of Coprini. (The subtribal names of Janssens are generally emended to terminate in -ina rather than -ides; thus, Phanaeides is now written Phanaeina.) Since Janssens cited neither the constituent genera of his subtribes (except those in disagreement with the keys) nor bibliography, one can only assume that their taxonomic composition agrees with that cited by previous authors.

For the present I have avoided formal nomenclatural reference to the phanaeine genera as Phanaeina or as its nomenclatural equivalents (Phanaeini, etc.). Thus, my collective references to this group of genera (phanaeines, phanaeine Scarabaeinae, etc.) are intended to be informal recognition of a taxon roughly equivalent taxonomically to Phanaeina (= Phanaeides = Phanaeini) of authors. My principal reason for at least temporarily side-stepping adoption of a formal name is the serious deficiency in our understanding of the interrelationships of other genera currently embraced by Coprini as they bear upon the taxonomic position of phanaeines. I have, thus, reluctantly concluded that Janssens' classification, at least as applicable to Coprini, can at best be used with caution, pending its intensive re-examination. Presently it suffices to say that I consider the phanaeine genera discussed below a monophyletic taxon characterized by the following features:

1. Antennal club three-segmented; basal lamella more-or-less scoop-shaped and enclosing, at least partially, the two distal lamellae; club usually large and spherical, but in *Dendropaemon* often flattened, elongate.

2. Dorsal surface of clypeus at least partially (usually wholly) transversely ridged.
3. Eyes (compound) completely divided into upper and lower portions by extension of paraocular areas of the parietals ("genae").
4. Front tarsi lacking in males; present or absent in females.
5. Middle and hind tarsi present, usually five-segmented, claws absent.
6. Metepisternal tab present.
7. Medial portion of metasternum acuminate anteriorly, often flattened and pentagonal ("rhomboidal").
8. Elytral interstriae usually convex, smooth or punctate.
9. Secondary sexual dimorphism usually strongly pronounced, sexes being easily distinguished by configuration of cephalic and pronotal protuberances, ridges, etc.
10. Size variable, usually 10-30 mm; typically robust; colors often partially or wholly metallic.
11. Eggs laid singly in earth-covered brood balls (see Halffter and Matthews, 1966).
12. Restricted to New World, mainly neotropical.

Olsoufieff's monograph (1924) is still the only comprehensive treatment of the phanaeine species. It has, moreover, been the basis of all subsequent treatments (including this one). Olsoufieff evidently had access to most of the known phanaeine type material, and his species descriptions and keys to species are the standards. There are, however, a number of works postdating his which complement it or enlarge upon its reliability as an identification manual. Among them are these: Barattini and Sáenz (1961, 1964; *Gromphas*), Blackwelder (1944), Blut (1939), Martínez (1944, 1959), Martínez and Pereira (1967), Pereira (1949), Pereira and Martínez (1956), Pessoa (1934, 1935), Pessoa and Lane (1936, 1941), Robinson (1947) and Vulcano and Pereira (1967:565 ff). The supraspecific classification presented here differs from that of Olsoufieff in the following respects:

1. Splitting of *Phanaeus* into three genera. The following outline shows the general changes, details of which are brought out below:

Olsoufieff (1924)	Present
Genus *Phanaeus*	
Subg. *Sulcophanaeus*	Genus *Sulcophanaeus*
Subg. *Phanaeus, sen. str.*	Genus *Phanaeus*
	Genus *Coprophanaeus*
Subg. *Megaphanaeus*	Subg. *Megaphanaeus*
Subg. *Metallophanaeus*	Subg. *Metallophanaeus*
Subg. *Coprophanaeus*	Subg. *Coprophanaeus, sen. str.*

2. Division of *Oxysternon* and *Dendropaemon* into two and three subgenera, respectively.
3. Recognition, where practical, of species-groups within generic categories. (This was attempted formally by Olsoufieff only for *Phanaeus, sen. str.*)
4. Removal of *Bolbites, Gromphas* and *Oruscatus* from the phanaeine assemblage.

Removal of *Bolbites, Gromphas* and *Oruscatus* from "Phanaeina" is done confidently but, at the same time, reluctantly since their alternative positions in the current classification of Coprini are not in the least clear. The rather strict definition of phanaeines given above definitely excludes *Gromphas* and *Oruscatus,* at least morphologically. Both are probably more closely related to dichotomines or, perhaps, to Old World elements which I have not studied. Nevertheless, as far as the South American fauna is concerned, both are taxonomic isolates, closely related neither to each other nor to other extant groups with which I am familiar. *Bolbites onitoides* Har. (monobasic), on the other hand, may later prove to be a phanaeine in some wider taxonomic sense than that presently used. It appears to show features of both phanaeines (some aspects of head structure, general body shape, metepisternal tab, etc.) and nonphanaeines (presence of tarsal claws, antennal club not of *Phanaeus*-type, etc.). It could very well happen that this species will prove to be highly important in assessing the position of phanaeines relative to the rest of the tribe. Nevertheless, firm placement of these three genera must await a thorough re-examination of Coprini on a world-wide basis.

The following classification is based upon phenetics and, therefore, subject to an inherent degree of inadequacy. The implicit hope is, of course, that the characters used, although a small sample of those potentially available, have been selected and studied sufficiently well that results based upon them will be supported by newly discovered characters. The terminology used in generic descriptions, keys, etc., is that established above; in doubtful instances, readers should refer to the two preceding sections. Some character states describing genera are numbered as are their definitions in part III; salient features are italicized in generic descriptions.

A potential source of inconvenience is that I was able to examine very little type material. The result could be perpetuation of a certain amount of nomenclatural confusion attending the names of some of the more poorly known species. I suspect that the greatest potential for error lies in the genus *Dendropaemon,* most of the species of which are only poorly known and subject to conflicting descriptions and usage in the literature. Nevertheless, on the whole I do not anticipate a great deal of subsequent need for correction since the majority of species names have been used quite consistently for many years. Moreover, during the course of this study, I consulted vari-

ous workers who together have examined a great deal of the available type material; among them is Padre F. S. Pereira of São Paulo.

Below is an outline of the classification proposed in the remainder of this part:

Genus *DIABROCTIS* Gistel
Genus *SULCOPHANAEUS* Olsoufieff
  faunus-group
  imperator-group
  auricollis-group
Genus *PHANAEUS* MacLeay
  splendidulus-group
    palaeno-complex
    endymion-complex
    chalcomelas-complex
    splendidulus-complex
    bispinus Bates (an isolate)
  vindex-group
    vindex-complex
    mexicanus-complex (comprising several species-clusters)
Genus *OXYSTERNON* Castlenau
  Subgenus *OXYSTERNON, sen. str.*
    festivum-group
    sericeum-group
  Subgenus *MIOXYSTERNON* NEW SUBGENUS
Genus *COPROPHANAEUS* Olsoufieff
  Subgenus *MEGAPHANAEUS* Olsoufieff
  Subgenus *METALLOPHANAEUS* Olsoufieff
  Subgenus *COPROPHANAEUS, sen. str.*
    jasius-group
    dardanus-group
Genus *DENDROPAEMON* Perty
  Subgenus *PARADENDROPAEMON* NEW SUBGENUS
  Subgenus *COPROPHANAEOIDES* NEW SUBGENUS
  Subgenus *DENDROPAEMON, sen. str.*
    denticollis-group
    viridipennis-group
    piceum-group
Genus *TETRAMEREIA* Klages
Genus *HOMALOTARSUS* Janssens
Genus *MEGATHARSIS* Waterhouse

Artificial Key to the Genera of Phanaeine Scarabaeinae

The following key is meant principally for purposes of identification. An effort has been made to select those character states most easily seen. Infrageneric taxa are separated in discussions of genera.

1. Middle and hind tarsi each with fewer than five segments; front tarsi always absent in female 2
– Middle and hind tarsi five-segmented; front tarsi present or absent in female 3
2. Middle and hind tarsi four-segmented, fourth (distal) segment very small (Fig. 263); clypeus not emarginate medially (Fig. 95); body robust (Figs. 312-313), color red-brown ..... *Tetramereia* Klages
– Middle and hind tarsi either two or three-segmented (Figs. 270-279); clypeus emarginate medially (Figs. 89-94); body robust to flattened (Figs. 304-309); color usually at least partially metallic blue or green ..... *Dendropaemon* Perty
3. Dorsal surfaces of hind tibiae and basal four hind tarsal segments covered by large, setigerous granules (Fig. 260); tarsal segments as in Figures 264 and 265; color dull metallic green; body robust (Figs. 310-311) ..... *Homalotarsus* Janssens

– Dorsal surfaces of hind tibiae and tarsi glabrous or with small setigerous granules; body robust, color variable 4

4. Labial palpus comprising a single oval segment (Figs. 154-155); dorsal surface of hind tibiae (Fig. 266) and abdominal sterna (Fig. 301) bearing dense fringes of rather long setae ..... *Megatharsis* Waterhouse

– Labial palpi three-segmented; tibiae and abdominal sterna without dense fringes 5

5. Anterior margin of clypeus emarginate medially (Figs. 83-89), clypeal process U-shaped; front tarsi usually absent in female; front tibiae as in Figure 246 ..... *Coprophanaeus* Olsoufieff

– Anterior margin of clypeus not emarginate medially (Figs. 98-110), clypeal process never U-shaped; front tarsi rarely absent in female; front tibiae variable (Figs. 250-259) but not as in Figure 246 6

6. Transverse clypeal carina present (Figs. 194, 197); transverse hind tibial carina present; large, green species ..... *Diabroctis* Gistel

– Transverse clypeal carina absent; hind tibial carina rarely present; size and color variable 7

7. Antero-median angle of metasternum prolonged as a long, sharp spine extending between apices of the front coxae (Figs. 244-245); postero-median angle of pronotum acute, distinctly prolonged between bases of elytra (Fig. 210) ..... *Oxysternon* Castlenau

– Antero-median angle of metasternum not spinate; postero-median angle of pronotum not distinctly prolonged 8

8. Occipital ridge absent or incomplete; anterior portion of circumnotal margin not broken by emarginations behind eyes (Figs. 117C, 121C-122C) ..... *Sulcophanaeus* Olsoufieff

– Occipital ridge complete (Figs. 1, 4); anterior margin of circumnotal ridge distinctly interrupted by emarginations receiving postocular lobes of parietals (Figs. 35, emarg; 36-38) ..... *Phanaeus* MacLeay

Genus **Diabroctis** Gistel

Diabroctis Gistel, 1857: 604. Type: *Scarabaeus mimas* L., original designation.
Taurocopris Olsoufieff, 1924:18. Type: *Scarabaeus mimas* L., present designation.

Until recently this genus has been known as *Taurocopris* Olsoufieff; the generic synonymy, *Taurocopris* = *Diabroctis,* was established by Martinez and Pereira (1967). Olsoufieff designated no type-species for *Taurocopris.* In order to stabilize the use of these names by precluding future question about their synonymy, it seems appropriate to hereby designate as the type-species of *Taurocopris* Olsoufieff (1924) the following species: *Scarabaeus mimas* L. By so doing, *Taurocopris* automatically becomes a junior objective synonym of *Diabroctis* Gistel.

DESCRIPTION

(1) *anterior margin of clypeus not emarginate medially,* strongly toothed (Figs. 98-99); (2) clypeal process transverse; lateral clypeal carinae well developed; *transverse clypeal carina present* (Figs. 194, 197, tcrcly); (3)

cephalic process of male lamellate, *a transverse ridge prolonged on each side into acute "horn"* (Figs. 194-195) (except *mirabilis* where lateral prominences greatly prolonged); (4) cephalic process of female carinate (Fig. 197); (5) paraocular areas of parietals narrow; (6) postocular lobes of parietals depressed transversely (Fig. 115B), anterior portion circumnotal margin not emarginate (115C); canthal area distinct (Fig. 115A, ca); (7) cephalic brachium monopodal; (8) eyes small; (9) occipital ridge incomplete, represented only by lateral segments; (10) *labrum Phanaeus-type;* (11) mentum strongly emarginate; (12) median lobe of hypopharynx present; (13) *premental sclerites marginally sclerotized;* (14) pronotum of male type C (Figs. 194-195); (15) pronotum of female type D (Fig. 196); (16) pronotum punctate (rugose antero-laterally in *mimas*); posterior pronotal fossae present (except *mirabilis*), large; (17) *front tarsi present in female;* (18) *front tibiae type C* (Fig. 250); *hind tibiae carinate laterally* (as in Fig. 262); (19) middle and hind tarsi five-segmented; (20) elytral interstriae smooth and (21) evenly convex; (22) striae simple; hind wing not notched; *color dark, dull green to metallic yellow-green;* size large (length 25-40mm).

The three species included in *Diabroctis* (*mimas* [L.], *cadmus* [Har.], *mirabilis* [Har.]) are easily recognized by their green color, large size and a transverse clypeal carina anterior to the cephalic process. *D. mimas* and *cadmus* are among the largest phanaeines (40 mm) and appear to be closely related; the male prothorax of these species (Figs. 194-195) is exceptionally massive. *D. mirabilis* differs from its congeners in the features brought out above, the most striking of which is the massive, antler-like development of the male cephalic process. All species have a distinct fringe of setae projecting from the elytral suture (the setae insert on the elytral margins), which is very prominent in *mirabilis*. Some species of *Phanaeus* (e.g., *demon*) have such fringes.

Diabroctis is restricted to South America; although *cadmus* has been cited (erroneously?) from Costa Rica (Gillet, 1911; Blackwelder, 1944), it is probably only South American (Colombia). *D. mimas* occupies an enormous range essentially determining the distributional limits of the genus while *mirabilis* is common only in southern Brazil and adjacent regions. A map of the range of *Diabroctis* is not given since it would look essentially like that given for *Oxysternon, sen. str.* (Map 3). Little is known about the biology of *Diabroctis* but it appears basically coprophagous. Both *mimas* and *mirabilis* have been collected in large numbers from human and bovine feces; *mimas* is often collected in swine feces in Manaus, Amazonas (Brazil).

Genus **Sulcophanaeus** Olsoufieff

Sulcophanaeus Olsoufieff, 1924: 23 (as subgenus of *Phanaeus*). Type: *Scarabaeus sulcatus* Drury = *Scarabaeus carnifex* L., 1758, not 1767, original designation.

Olsoufieff (1924: 23) designated *Phanaeus sulcatus* (Drury) as the type-

species of the subgenus *Sulcophanaeus*. The name *sulcatus* Drury has since been recognized as a junior subjective synonym of *carnifex* L., 1758 (Matthews, 1966: 39). Consequently, the valid name of the type-species of this genus becomes *Phanaeus carnifex* (L.), 1758. It should be noted that, pending a ruling by the International Commission on Zoological Nomenclature, the name *Sulcophanaeus* could later be ruled a junior objective synonym of *Onthurgus* Gistel (see discussion below in introduction to *Phanaeus*).

DESCRIPTION

(1) anterior margin of clypeus not emarginate medially (Figs. 102-105); (2) clypeal process transverse, either tooth-like or ridge-like; lateral clypeal carinae usually present; (3) cephalic process of male corniform (Figs. 198, 203-204, 209); (4) cephalic process of female corniform or carinate (Figs. 199, 201-202, 205, 207); (5) paraocular areas of parietals narrow; (6) postocular lobes of parietals depressed transversely (part B of Figs. 117, 121-122), circumnotal ridge not interrupted by emarginations (parts C of same Figs.); canthal area usually distinct (Fig. 117); (7) cephalic brachium monopodal (bipodal in few species); (8) eyes small; (9) occipital ridge incomplete; (10) labrum *Phanaeus*-type; (11) mentum strongly emarginate (Fig. 158); (12) median lobe of hypopharynx present; (13) premental sclerite marginally sclerotized (Fig. 150); (14) pronotum of male variable (Figs. 198, 203-204, 206, 209); (15) pronotum of female type C or D (otherwise in *faunus* group, Figs. 199-200); (16) pronotum smooth (rugose in *laeander* and *columbi*); antero-lateral angles of pronotal ridge often angulate; posterior pronotal fossae present (except *actaeon*); (17) front tarsi present in female (except *carnifex* and, reportedly, *steinheili*); (18) front tibiae *Phanaeus*-type; transverse hind tibial carinae sometimes present; (19) middle and hind tarsi five-segmented; (20) elytral interstriae smooth and (21) flat or convex; (22) striae simple; hind wing not notched.

The name *Sulcophanaeus* is used here in a much different sense from that used by Olsoufieff (1924). In the subgenus *Sulcophanaeus* Olsoufieff included only two species, *carnifex* (as *sulcatus*) and *steinheili,* which reportedly resembled each other in the structure of the male genital capsule and lack of front tarsi in the female; but he was doubtful about the soundness of his grouping. In the present sense *Sulcophanaeus* brings together a rather diverse group of species including not only the above two but also a large number included by Olsoufieff in *Phanaeus, sen. str.* (all of species group 1, species group 2 [except *bispinus*] and part of species group 3). The genus forms three species groups which, because of their distinctness, would likely warrant consideration as subgenera if the genus were larger. While these species groups are certainly distinct, it is noteworthy that each, *inter*

se, comprises more or less readily recognizable isolated elements (phenetically and often geographically) mostly as single species or species pairs.[11]

Key to the Species Groups of **Sulcophanaeus**

1. Both sexes with well developed corniform cephalic processes, that of the male very long, curved, tapering (Fig. 198), that of the female either similar to male (*faunus,* Fig. 199, and *columbi*), strongly bifurcate *(laeander)* or as in Figures 201 and 202 *(carnifex)*; paraocular areas of parietals each strongly carinate above lateral to eye; postocular lobes of parietals, seen laterally, extended anteriorly as finger-like process (Fig. 117A) approaching upper portion of eye (except *carnifex*); clypeal process tooth-like (Fig. 113); lateral pronotal carina present (Figs. 199, 201, 203, lpc); elytral interstriae unevenly convex ("sulcate") (Fig. 283); large beetles, either uniform dull black brown or metallic green. ..... *faunus* group
– Cephalic process of male as above; that of female a simple or tuberculate carina (Figs. 205, 207); paraocular areas carinate or not; postocular lobes of parietals not projecting anteriorly; clypeal process ridge-like (except *rhadamantus*); lateral pronotal carina absent (except male *imperator*); elytral interstriae convex or flat; moderate sized (20-30mm), color variable 2
2. Paraocular areas of parietals not strongly carinate lateral to eye; front tibiae tridentate, teeth concentrated in apical 1/3 of outer margin (Fig. 251); elytral interstriae flat (Fig. 282), though sometimes with irregular wrinkling; pronotum of male flat or shallowly concave, sloping downward anteriorly from pair of closely set posteromedian processes (type F); pronotum of female convex except for anterior transverse ridge shaped as in Figure 207; elytra dull black (except *actaeon*), pronotum completely or marginally metallic. ..... *auricollis* group
– Paraocular areas of parietals carinate lateral to eye; apical three teeth of front tibiae occupying more than 1/3 outer margin; elytral interstriae convex; pronotum of male variable; pronotum of female variable; color variable ..... *imperator* group

The *faunus* group (*faunus* [F.]; *columbi* [MacL.]; *laeander* [Waterhouse]; *carnifex* [L.]): All these species are large insects (30+mm) and, in addition to the features mentioned in the key, resemble each other quite closely in general appearance of the head capsule. Although they are easily distinguishable, *columbi* and *laeander* form a loose species pair (rugose pronotum, metallic green color, bipodal cephalic brachium). Both, however, are clearly related to *faunus* (see Key), which at the same time shares a number of unique features with *carnifex* (strong transverse hind tibial carinae, uniform dull black-brown color, intrasternal position of last ab-

[11] In this and subsequent discussions a species pair is meant to refer to two species which are presumed more closely related to each other than either is to other members of a given taxon. In general the members of a pair are very closely related and sometimes difficult to separate (i.e., "sister species"), but this need not be so.

dominal spiracle). *S. faunus,* then, is an annectant species connecting otherwise quite different species. The general resemblance of *faunus* and *carnifex* is striking and was mentioned, but not stressed by Olsoufieff (p. 79).

S. carnifex is noteworthy in that, being endemic to Jamaica, it is the only phanaeine not a continental species. The most reasonable explanation for its presence there is that, like a number of other Jamaican scarabaeines (Matthews, 1966), it is an insular relict of probably very long standing residence. The relict status of *carnifex* as well as its ecology is discussed by Matthews (1966). The other species in this group are South American (see Map 1). The ranges of *laeander* and *columbi* are poorly known due to the rarity of these species in collections; the former is generally considered Venezuelan (a savanna species ?) while *columbi* has been collected in the southern part of the Amazon Basin. *S. faunus,* which is definitely a forest species, occupies a wide range in the Amazon Basin. Except for *carnifex,* the biology of these species is largely unknown. Matthews (1966) reports that *carnifex* is coprophagous, occurring in large numbers in cow dung, and likely restricted to certain soil types. This is the only instance where the possible limiting effects of edaphic factors upon phanaeines has been reported; the distributional effects of soil types on Scarabaeinae has so far been largely ignored. *S. columbi* has been collected from tapir feces (B. Malkin, pers. comm.) while *faunus* is reportedly necrophagous(Pereira, pers. comm.). I know nothing of the biology of *laeander,* but if it truly is a savanna species, I would expect it to be coprophagous.

THE *imperator* GROUP (*imperator* [Chevr.]; *steinheili* [Har.]; *rhadamantus* [Har.]; *batesi* [Har.]; *menelas* [Cast.]): This group consists of two species pairs and one species which appears taxonomically isolated. The latter species, *rhadamantus,* is extremely rare; only because it somewhat resembles *imperator* do I place it here. *S. batesi* and *menelas* (*splendidulus* of Olsoufieff and often so identified in collections) are very similar (unique shape of pronotum of both sexes, "sulcate" elytra), except for color differing only in minor details. A study of the geographic variation of this pair is in order since they could be subspecies. A rather close relationship between *imperator* and *steinheili* can be supported here only on the basis of the males (very similar pronota; presence of hind tibial carinae). This similarity was mentioned both by Harold (1875) and Olsoufieff (p. 79). I have not seen the female of *steinheili,* which, according to Olsoufieff, lacks front tarsi. This species pair only slightly resembles *menelas-batesi* in general facies. The presence of hind tibial carinae and lateral pronotal carinae link it with *faunus-carnifex,* which it resembles even less in general appearance. Moreover, *imperator* has a bipodal cephalic brachium, known elsewhere in the genus only in *laeander-columbi.* Such a mosaic appearance of features can

MAP 1. Approximate distributions of the species groups of *Sulcophanaeus*. Arrows connect widely disjunct portions of distributions.

be interpreted as either parallel evolution or a closer phyletic proximity than indicated by the classification; I have chosen the former interpretation.

The *imperator* group comprises largely temperate species. Except for *steinheili*, a rare species known only from the Bogotá region of Colombia, they occur in southern South America (Map 1). *S. imperator*, the southern relative of this species, is also a high altitude species inhabiting the higher Andean plateau regions of Argentina and Bolivia. The range of *batesi* approximates that of *imperator* while *menelas* occurs in the grassland regions of eastern and central Argentina and Bolivia and southern Brazil. *S. rhadamantus* is known from very few specimens, some from the state of Buenos

Aires, Argentina. Martínez (1959), reports that *imperator, batesi* and *menelas* are strictly coprophagous, preferring herbivore (livestock) excrement. The latter species, however, is evidently at least occasionally necrophagous (J. Foerster, pers. comm.).

THE *auricollis* GROUP (*auricollis* [Har.]; *chryseicollis* [Har.]; *noctis* [Bates]; *velutinus* [Murray]; *actaeon* [Erichson]): Of the species groups comprising *Sulcophanaeus* this is the most cohesive, phenetically and geographically. Three of the five included species, *auricollis, chryseicollis* and *noctis,* appear quite closely related, differing most obviously in color. While the pronotum of the male of *velutinus* is strikingly different from that of the above three species (cf., Figs. 206, 209), the pronotum of the females of all four are very similar, principally because of the unique shape of the anterior carina (Fig. 207). *S. actaeon,* the female of which I have not seen, differs from the above species in several respects, the most striking of which is its all metallic color. While the elytral interstriae are flat and dull black in other species, in *actaeon* they are irregularly raised (appearing "blistered") and metallic blue or green. To a much lesser degree, the "blistering" is seen in other species of the group, particularly *velutinus.* A curious feature of this group, seen also in some *Phanaeus,* is a tendency for the propleura to be hollowed for the reception of the posterior margins of the paraocular areas of the parietals. The depth of these concavities varies as does the size of the tubercle adjacent to each which fits beneath the paraocular area.

The center of distribution of this group appears to be the lowlands and foothills along the eastern slopes of the Andes from Panama southward through Peru (Map 1). One species, *chryseicollis,* is largely restricted to neotropical southern Mexico and is the only continental *Sulcophanaeus* not occurring also in South America. Both *noctis* and *velutinus* occur from Panama to Peru; *auricollis* is largely restricted to Colombia while *actaeon* is known to me from only a few Peruvian localities. None of these species, however, are well represented in recent collections with precise locality designation. Accordingly, in view of the tremendous physiographic variation of the general range of this group, very little is known of their ecological distribution within it. I have no ecological data on *actaeon* and *auricollis. S. chryseicollis* has been collected in southern Mexico at night using traps baited with human excrement (Halffter and Matthews, 1966). Both *noctis* and *velutinus* have been collected in the same manner from the Chiriquí region of Panama (D. Viers, pers. comm.).

Genus **Phanaeus** MacLeay

Phanaeus MacLeay, 1819: 124. Type: *Scarabaeus carnifex* L., 1767, not 1758 = *Phanaeus vindex* MacLeay, subsequent designation by Olsoufieff, 1924: 23, see discussion below.

Lonchophorus Germar, 1824: 126. Type: *Scarabaeus carnifex* L., 1767, not 1758 = *Phanaeus vindex* MacLeay, present designation.

Onthurgus Gistel, 1857: 602. Type: *Scarabaeus carnifex* L., 1767, not 1758 = *Phanaeus vindex* MacLeay, original designation (objective generic synonymy subject to opinion of the International Commission on Zoological Nomenclature, see below).
Phanaeus, sen. str., Olsoufieff, 1924: 23 (pars).

The following nomenclatural melodrama has emerged in determining the valid name of the type-species of *Phanaeus*. MacLeay (1819) designated no type-species for *Phanaeus*, nor were any of the included species indicated as type-species. Subsequently, Olsoufieff (1924: 23) designated as the type-species of *Phanaeus, sen. str.*, a North American species which he referred to as *P. carnifex* (L.). Although he rightly suspected that Linnaeus had used the name *carnifex* in at least two different senses (one in 1758, another in 1767), Olsoufieff nevertheless synonymized the names *carnifex* L. and *vindex* MacLeay (pp. 95 and 151). Matthews (1966: 41), in order to rectify the confusion attending the name *carnifex*, designated a lectotype fixing the name to a Jamaican species and thereby preserved Linnaeus's original usage of the name *carnifex* (1758). Consequently, *carnifex* becomes the valid name of the type-species of *Sulcophanaeus* (see above), and *vindex*, the only available synonym for *carnifex sensu* Linnaeus (1767) and Olsoufieff (1924), becomes the valid name of the type-species of *Phanaeus*. The following synonymies are based on several sources:

Sulcophanaeus carnifex (L.)
= *Scarabaeus carnifex* L., 1758: 346 (not 1767)
= *S. sulcatus* Drury, 1770
= *S. sphinx* Fab., 1772
= *S. belzebul* Fab., 1775
= *S. nicanor* Fab., 1781
= *S. lar* Herbst, 1789
= *Phanaeus moloch* MacLeay, 1819: 129 (species inquirenda)
= *P. sulcatus* (Drury), Olsoufieff, 1924: 23
Phanaeus vindex MacLeay
= *Scarabaeus carnifex* L., 1767: 546 (not 1758) (junior primary homonym)
= *Phanaeus vindex* MacLeay, 1819: 133 (species inquirenda)
= *P. vindex* MacLeay, 1833: 47 (from Gillet, 1911: 82)
= *P. carnifex* (L.), Gistel, 1857: 602
= *P. carnifex* (L.), Olsoufieff, 1924: 23, 39, 95, 151

The mistaken identity of *carnifex* L., 1767, by Linnaeus himself and subsequently by Olsoufieff, has resulted in a case of mis-identified type-species of a genus. In accordance with Articles 67 (j) and 70 (a) of the International Code of Zoological Nomenclature, I have requested that the International Commission on Zoological Nomenclature rule *Scarabaeus carnifex* L., 1767, not 1758, = *Phanaeus vindex* MacLeay the type-species of *Phanaeus* MacLeay. The use of the name *carnifex* by Olsoufieff is unquestionably in the sense of Linnaeus, 1767, hence in the sense of *vindex* MacLeay (see Olsoufieff, 1924: 95).

As for the name *Onthurgus* Gistel, the situation is not quite so simple.

Gistel (1857: 602) designated as the type-species of this genus *"Phanaeus carnifex* (L.)", leaving uncertain in which sense of Linnaeus (1758 or 1767) the name was used. The Code states (Art. 70) that one should assume that names designated as type-species of genera are used correctly unless there is evidence to suggest otherwise. To assume correct usage in this case would be to assume that Gistel used the name *carnifex* in the sense of Linnaeus, 1758, thereby requiring that *Onthurgus* be regarded a *senior* objective synonym of *Sulcophanaeus*. Since there are several reasons favoring the retention of the name *Sulcophanaeus* (particularly the taxonomic relationships implicit in the "phanaeus" part of the name), I have requested that the Commission 1) exercise its plenary powers to suspend Article 70 of the Code and rule that the type-species of *Onthurgus* Gistel is *Scarabaeus carnifex* L., 1767, not 1758, = *Phanaeus vindex* MacLeay and thereby effect the objective synonymy of *Onthurgus* and *Phanaeus* and/or 2) rule the name *Onthurgus* Gistel a *nomen oblitum* in accordance with Article 23 (b) of the Code since, to my knowledge, the name has never been used since 1857. A positive ruling by the Commission on either (1) or (2) will preserve the present usage of the name *Sulcophanaeus*.

DESCRIPTION

(1) *anterior margin of clypeus not emarginate medially,* usually toothed (Figs. 4, 105-110); lateral clypeal carinae almost always present; (2) clypeal process transverse (rarely spiniform); (3) cephalic process of male corniform (Figs. 1, 216, 218, 221, 226); (4) cephalic process of female carinate (Figs. 3, 79, 81-82, 220, 222); (5) paraocular areas of parietals narrow; (6) *postocular lobes of parietals depressed obliquely* (Fig. 4), *prominent, fitting in emarginations of circumnotal ridge* (Fig. 35, emarg; not distinct in *haroldi,* Fig. 119); canthal areas not distinct; (7) *cephalic brachium bipodal* (anterior arm reduced in some species, Figs. 129-130); (8) eyes small; (9) *occipital ridge complete* (Figs. 1, 4, 8, ocr); (10) labrum *Phanaeus*-type (Figs. 18-19); (11) mentum strongly emarginate (Fig. 25); (12) median lobe of hypopharynx present; (13) *premental sclerites completely sclerotized;* (14) pronotum of male type A or B (Figs. 35-36, 216-219, 221, 223-228); (15) pronotum of female type B or D (Figs. 37-38, 220, 227); (16) pronotal sculpturing punctate or roughened (Figs. 159, 161, 163-165); posterior pronotal fossae usually present; (17) front tarsi present in female (Figs. 61, 63); (18) front tibiae tridentate or quadridentate (Figs. 60-61, 256-259); (19) middle and hind tarsi five-segmented (Figs. 64-66); (20) elytral interstriae smooth (Figs. 285-287) or rugose (Fig. 284); (21) interstriae flat or evenly convex; (22) striae usually simple; hind wing not notched (except *bispinus*); last abdominal spiracle marginal; color only rarely not at least partially metallic.

The name *Phanaeus* is used here in a more restricted sense than has

heretofore been customary. It is roughly equivalent taxonomically to species groups 3 and 4 of the subgenus *Phanaeus, sensu* Olsoufieff (1924). Taxonomically *Phanaeus* is the most difficult phanaeine genus because of the high incidence of irregular distribution of character states and of continuous variation of characters reliable (i.e., with discrete states) in other genera. Thus, there exist in the genus (particularly evident in the *mexicanus* complex) extremes which definitely warrant taxonomic recognition; but, on the other hand, separation of the extremes is precluded by an array of intermediate forms. In the interest of a balanced classification, I have concluded it advisable to recognize only informally what appear to be the constituent taxa of this genus. I have, therefore, used freely the following categories: species-group, species-complex and species-cluster. Further study using more characters will be necessary before the applicability of more formal categories (e.g., subgenus) can be determined.

Key to the Species Groups and Species Complexes of **Phanaeus**

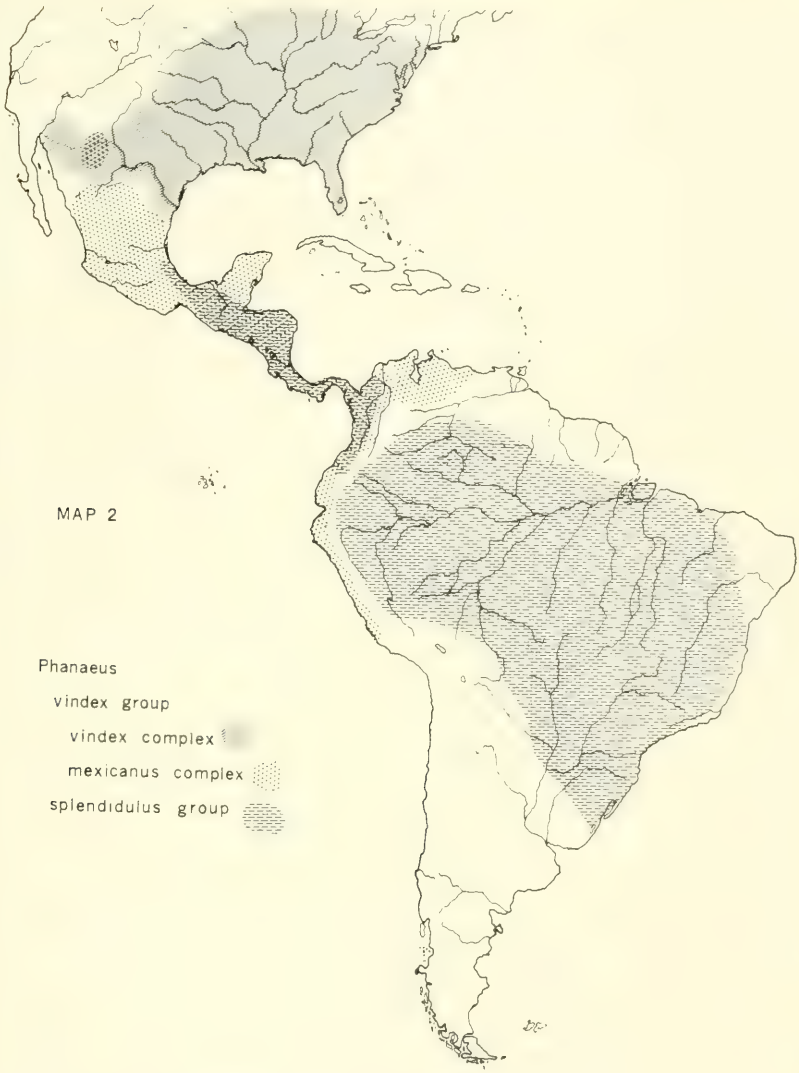
1. Pronotum evenly, strongly roughened (granulate to rugose) at least antero-laterally but often entirely so; punctures, if present, restricted postero-medially; cephalic process of female an isolated carina or thick ridge (Fig. 82) (except *hermes* cluster); pronotum of male with prominent postero-lateral angles, usually appearing more-or-less triangular from above ..... *vindex* group 6
   – Pronotum completely or largely punctate, often appearing glassy smooth and shining, at most with irregular gibbosities (except female of *meleagris*) or minutely granulate (males of *endymion* complex); cephalic process of female a transverse, usually trituberculate carina extending fully between mesal ends of lateral clypeal carinae (Fig. 81); pronotum of male variable ..... *splendidulus* group 2
2. Pronotum of male with close-set pair of parallel, elongate processes (as in Figs. 214-215); that of female with a single such process projecting forward from middle of posterior margin of an antero-median concavity; elytral striae carinulate, distinctly punctured; hind wing deeply notched; dorsum dull greenish-brown ..... *bispinus* Bates
   – Pronotum of male as in Figures 216-219, 221; that of female as in Figures 220, 222; elytral striae variable; hind wing not notched; color variable 3
3. Clypeal process small, spinate; cephalic process of small males a short, bituberculate process; elytral striae carinulate, not punctate; dorsum dark, highly shining green; anterior margin of clypeus strongly toothed medially; venter often bearing long, whitish hair .. *palaeno* complex
   – Clypeal process variable, not spinate; cephalic process of small males never a bituberculate process; other characters variable 4
4. Front tibiae of female quadridentate (Fig. 256), resembling *Copro-phanaeus*-type; anterior margin of clypeus strongly toothed medially (Fig. 108); pronotum of male *very* flat dorsally, produced postero-laterally and appearing triangular from above (Figs. 218-219), sometimes very finely and irregularly granulate dorsally but

usually appearing smooth without magnification; pronotum of female smooth, without granulation ..... *endymion* complex
– Front tibiae of female tridentate; anterior margin of clypeus at most only weakly toothed medially; other characters variable 5
5. Elytral striae carinulate, distinctly punctate; pronotum bearing irregularly spaced gibbosities dorsally, punctate antero-laterally (more-or-less evenly, though not strongly rugose in *meleagris*); clypeal process not tooth-like; pronotum of male very flat dorsally, produced postero-laterally and appearing triangular from above; dorsum yellow-brown ("bronze") or nearly black .... *chalcomelas* complex
– Elytral striae simple, not punctate; pronotum punctate or smooth; clypeal process tooth-like (as in Fig. 113): pronotum of male deeply concave dorsally (Fig. 217); color variable ..... *splendidulus* complex
6. Elytral interstriae rugose (Fig. 284) or (seen magnified) distinctly heavily punctured, punctures coalescent ..... *vindex* complex
– Elytral interstriae smooth or only very finely punctured (Figs. 285-286) ..... *mexicanus* complex

THE *splendidulus* GROUP: This is essentially a South American group (Map 2) the members of which fall rather neatly into the species complexes separated above. The *palaeno* complex is a species pair (*palaeno* Blanch. and *kirbyi* Vigors); *palaeno* bears a striking resemblance to *Oxysternon palaemon*, the two species forming the only potential intergeneric mimic-model complex among phanaeines. Both species of this complex occur (sympatrically ?) in the savanna-turned-pasturelands of southern Brazil and adjacent regions; *palaeno* (and also *kirbyi* ?) is very common in cattle feces.

The *endymion* complex includes three closely related species (*endymion* Har.; *pyrois* Bates; *blanchardi* Ols.) with quadridentate front tibiae resembling those of *Coprophanaeus*. Both *endymion* and *pyrois* occur in tropical lowland forests of Central America and southern Mexico and are the only yet described members of the *splendidulus* group occurring outside mainland South America. These two species have been collected from traps baited with human feces. I know *blanchardi* from a single locality in Ecuador ("Pucay"). There is a fourth, yet undescribed species likely belonging in this complex which I know from a single, well developed male collected near Temascaltepec, Mexico (state of Mexico) by H. E. Hinton. The male in question is evidently one of several individuals collected by Hinton from a decomposing hymenomycete fungus (probably a toadstool) (Hinton, 1935). Although referred to by him as *endymion*, which the new species closely resembles, Hinton's illustration is undoubtedly of a well developed male of the same new species, not *endymion*. (*P. funereus* Balths. is an unassigned name probably belonging in this complex.)

The *splendidulus* complex includes three rather closely related species (*splendidulus* [Fab.], *dejeani* Har. and *melibaeus* Blanch.) in addition to *haroldi* Kirsch. The first two species have been collected from cow dung in



MAP 2. Approximate distributions of the species groups of *Phanaeus*.

the Serra do Mar region of southern Brazil but neither appears restricted to the area. Some confusion exists with locality data under the name *splendidulus* since until recently the name was erroneously applied to *Sulcophanaeus menelas*. *P. melibaeus* is restricted to the southern Amazon Basin where it has been collected in dung. The shape of the pronotum and aspects of head structure set *haroldi* apart from other members of the complex; I have in-

cluded it here, perhaps artificially, on the basis of its closer resemblance to *melibaeus* than to any other species in the group. The range of *haroldi* appears concentrated in the tropical lowland valleys along the eastern slopes of the Andes (Colombia, Ecuador and Peru).

The *chalcomelas* complex is a species pair (*chalcomelas* Perty and *meleagris* Blanch.). The former is a widespread Amazon Basin species which is reportedly coprophagous (Halffter and Matthews, 1966: 31). It and *meleagris*, a necrophagous species (*loc. cit.*, 31), bear distinct, though usually irregular gibbosities over the surface of an otherwise punctate pronotum which suggest the pronotal roughening of the *vindex* group.

Phanaeus bispinus Bates (an isolate of complex rank) resembles both *chalcomelas* (carinulate-punctate elytral striae, color) and *haroldi* (shape of cephalic process and other aspects of head structure), but several unique features support its taxonomic isolation with the *splendidulus* group: shape of the pronotum of the male (not unlike that of *Oxysternon curvispinum*, Figs. 214-215) and of the female (which is unlike any other phanaeine, a single elongate process in place of the paired processes of the male) and notching of the hind wing (seen otherwise only in some *Coprophanaeus* and in *Dendropaemon*). I have seen few specimens of *bispinus*, all from the Amazon Basin; Pereira and Martínez (1956) say it is necrophagous.

THE *vindex* GROUP: This species group includes the bulk of those species here assigned to *Phanaeus* (32 of 44 species). Most are North American species (Map 2).

The *vindex* complex includes four species with either rugose or heavily punctured elytral interstriae. The rugosity of the elytra is strongest in *vindex* MacL. (Fig. 284) and *difformis* Lec.; in *igneus* MacL. (= *floridanus* Ols.) and *triangularis* Say (= *torrens* Lec.), however, the elytral rugosity tends to be effaced and evident only with magnification as dense, confluencent puncturing. All four species are predominantly coprophagous and commonly collected in cattle feces in pastures. *P. igneus* and *triangularis* are endemic to the United States (particularly the southeast); the ranges of *vindex* and *difformis*, while centered in the United States, extend into northern Mexico.

The *mexicanus* complex brings together a relatively large number of species whose combined ranges extend from northwestern South America to the southwestern United States (Map 2). Most are endemic or largely endemic to tropical Mexico and adjacent Central America. All included species whose feeding habits are known are normally coprophagous although their ecological distribution (horizontal and vertical) appears quite wide. The *mexicanus* complex remains in need of revision at the species level using more characters than those employed here; a detailed study of these species including geographic variation and reference to type material

could well result in reduction to subspecific rank or synonymy of some of the species cited below. I have little doubt that the *mexicanus* complex is a natural group in spite of the fact that my study so far has produced no sound basis for assessing the interrelationships among the constituent clusters of obviously closely related species. I find that character states that are normally fixed in other phanaeine taxa of comparable size and/or rank (e.g., various aspects of integumental sculpturing) vary in a seemingly irregular pattern among these clusters. Still the only satisfactory way, albeit taxonomically unsatisfying to me, of distinguishing closely related species is by differences in secondary sexual features of well developed males (particularly pronotal shape). The very striking phenetic similarity of small males and females of closely related species attests to a degree of virtual siblingness unapproached in any other phanaeine taxon. Identification of potentially sibling individuals can at best only be inferred, and then only if they form parts of a sample including well developed males.

Following are diagnoses of the species-clusters comprising the *mexicanus* complex; included are two isolated species treated as of cluster rank. In general, the species of each cluster resemble each other in at least the following respects: shape of male pronotum, relief of elytral interstriae (flat or convex); pronotal sculpturing (granulate or rugose) and great similarity of females. I have avoided compiling a key to species-clusters since variation of characters used would render it largely inefficient and little better than that of Olsoufieff (1924: 37-46).

Cluster 1 (*lugens* Nev., *prasinus* Har., *hermes* Har.): Prothorax evenly granulate; male pronotum as in Figures 223-224; female pronotum convex, with three flat antero-median tubercles; elytral interstriae weakly convex, striae distinctly punctate (seen under 10× magnification). Besides striking interspecific female similarity, the males very closely resemble each other; the most conspicuous variation distinguishing most individuals of either sex is color. Both *prasinus* and *lugens* occur in Venezuela and adjacent regions of Colombia; *hermes* ranges from Colombia into Central America.

Cluster 2 (*mexicanus* Har., *amythaon* Har., *wagneri* Har., *lunaris* Faschb.): Prothorax rugose, less heavily so in female; male pronotum as in or similar to Figure 226; female pronotum as in Figure 227, with low-set, transverse antero-median ridge flanked by shallow, usually smooth concavities; elytral interstriae convex, striae simple or very weakly punctate. I cannot reliably identify females or small males of these species unless they are collected along with well-developed males of a single species; well-developed males differ in subtle features of pronotal shape. The distribution of this cluster is unique, the composite range extending from Peru to Arizona: *lunaris* occurs in eastern Peru (and Ecuador ?), *wagneri* is largely

Central American, *mexicanus* is very common in southern Mexico while *amythaon* has been collected from southwestern Mexico northward along the western seaboard of Mexico into Arizona (Prescott).

Phanaeus achilles Bohart: I have seen one well developed male of this species; it resembles the males of cluster 2 in all respects except color (bright red above) and strong puncturing of the elytral striae. It is known from Peru and Ecuador.

Cluster 3 (*demon* Har., *obliquans* Bates): Pronotum rugose except dorsally; male pronotum (see below); female pronotum as in Figure 227; elytral interstriae weakly convex, striae simple; leading margin of head distinctly notched at lateral extremity of each postclypeal carina (Fig. 109). The pronotum of the male of *demon* is unique in the genus (Fig. 225); the postero-lateral angles are produced as massive projections (which are acute and slanted posteriorly in *obliquans*) flanking a deep, smooth median concavity. Both species are ordinarily of a green color much more highly shining than the usually dull metallic colors of other species in the complex. *P. demon* is very common in the hot tropical valleys (e.g., of Río Balsas) of southern Mexico; I know *obliquans* only from a few Central American localities.

Cluster 4 (*quadridens* Say, *damocles* Har.): Pronotum rugose; pronotum of female convex, with transverse anteromedian ridge; elytral interstriae flat, shining, striae nearly effaced (Fig. 286). The pronotum of male *quadridens* is flat above with large, flaring postero-lateral angles; that of male *damocles* closely resembles that of cluster 5 (see below). Both species are evidently restricted to higher altitudes in Mexico; *quadridens* is characteristic of the Mexican Plateau (see Halffter, 1964), where few other *Phanaeus* are encountered, while *damocles* is found in pine-oak forests in southern Mexico (Halffter, pers. comm.).

Cluster 5 (*palliatus* Sturm, *eximius* Bates): Pronotum rugose; male pronotum shaped as in Figures 223-224 except that dorsal surface concave with median tubercle; pronotum of female as in cluster 4; elytral interstriae convex, striae simple. This species pair is perhaps to be regarded as an annectent among clusters 5, 7 and 8. I have seen very few *eximius*, all from Central America; *palliatus* is also generally regarded as rare although it can be found in numbers in isolated localities in the mountains near Mexico City. G. Halffter and I collected many specimens of *palliatus* from burro and human dung near Ocoyoacac (state of Mexico); Halffter feels that it is narrowly distributed altitudinally. The variation in color of *palliatus* is striking; in the single Ocoyoacac sample are bright metallic red, green and dark blue individuals of both sexes.

Cluster 6 (*pilatei* Har., *sallei* Har., *beltianus* Bates, *flohri* Nev.): Pronotum rugose; shape of pronotum of well developed males similar to cluster

1 but with very smooth, triangular area basally; pronotum of female convex, with small transverse antero-median ridge; elytral interstriae convex, striae simple. This cluster is evidently restricted to Central America and adjacent regions of Mexico. Although I have seen only a few specimens of each, I suspect that of the four names listed, only two will remain full species upon serious study. I know nothing of the biology of these species.

Cluster 7 (*guatemalensis* Har., *amethystinus* Har., [probably = *martinezi* Halffter], *scutifer* Bates, *melampus* Har.): Pronotum rugose; pronotum of well developed males similar to Figures 223-224, with smooth basal area bearing small acute tubercle anteriorly; pronotum of female convex, with medially dentate ridge anteriorly; elytral interstriae convex, striae simple. These species are very similar; all except *scutifer* (likely a color variation of *guatemalensis*) are dull or blue-black. As in cluster 6, these species are restricted to southern Mexico and Central America.

Phanaeus adonis Har.: This species, relatively common in valleys along the southern periphery of the Mexican Plateau (Halffter, pers. comm.), resembles *triangularis* more than any Mexican species. As in *triangularis*, the male pronotum is flat dorsally and strongly produced postero-laterally and the pronotum of both sexes is coarsely granulate. Unlike the *vindex* complex, however, the elytral interstriae are at most weakly punctured.

Cluster 8 (*daphnis* Har., *tricornis* Ols., *tridens* Cast., *nimrod* Har., *furcosus* Bates): Pronotum rugose; pronotum of well-developed males with rounded postero-lateral angles, concave dorsally with usually large median or basal process of varying shape, sides of concavity serrate and/or dentate (Fig. 228); pronotum of female convex, with small antero-median ridge; elytral interstriae convex, striae simple. All these species are relatively small (to 15mm in length) and usually wholly green or yellow-green. I cannot reliably separate females and most small males of this cluster without corroborating evidence; of the subtle pronotal features distinguishing well developed males, the shape of the median process is most conspicuous. This cluster occurs from southern Mexico northward along the western coast of Sinaloa.

Unassigned names probably belonging in the *Phanaeus mexicanus* complex: *goidanichi* Balths., *pseudofurcosus* Balths., *substriolatus* Balths., *frankenbergeri* Balths., *babori* Balths.

Genus **Oxysternon** Castlenau

DESCRIPTION

Dorsal surface of clypeus completely transversely ridged or punctate posteriorly; (1) anterior margin of clypeus not emarginate medially, at most weakly toothed (Figs. 210, 213-214); (2) clypeal process transverse, spiniform (Fig. 112) or reduced; lateral clypeal carinae present or absent; (3)

cephalic process of male corniform (Figs. 210-211) or reduced to a short bituberculate process or two simple tubercles; (4) cephalic process of female a simple or tuberculate carina; (5) paraocular areas of parietals narrow; (6) shape of postocular lobes of parietals as described in part III, anterior portion of pronotal ridge effaced (*Mioxysternon*) or weakened or broken by shallow emarginations; canthal area distinct or not; (7) cephalic brachium bipodal (not observed for *Mioxysternon*); (8) eyes small; (9) *occipital ridge complete;* (10) *labrum Phanaeus*-type; (11) mentum strongly emarginate; (12) median lobe of hypopharynx present; (13) *premental sclerites completely sclerotized;* (14) pronotum of male as in Figures 210-211 or 214-215; (15) pronotum of female type D (Figs. 212-213); (16) pronotum punctate (Fig. 160), often appearing completely smooth; *postero-median angle of pronotum distinctly produced as acute process fitting between inner basal angles of elytra* (Fig. 210), *posterior pronotal fossae absent* (except ? *biimpressum Ols.*); *antero-median angle of metasternum strongly produced as acute spine fitting between front coxae* (Figs. 244-245); (17) front tarsi present in female; (18) front tibiae tridentate or quadridentate; (19) middle and hind tarsi five-segmented; (20) elytral interstriae smooth to punctate and (21) evenly convex (Figs. 280-281); (22) striae simple, sometimes nearly effaced; hind wing not notched; seventh abdominal spiracle marginal or intrasternal.

In addition to the above features there is a tendency among species of *Oxysternon* for abdominal sternum 7 to be almost vertical relative to sternum 6, such that, seen in profile, the abdomen has a decidedly angulate appearance.

KEY TO THE SUBGENERA AND SPECIES GROUPS OF **Oxysternon**

1. Cephalic process of male two closely-set median tubercles (Fig. 80), that of female either absent or a weak, sometimes tuberculate carina; clypeal process reduced to small tubercle; lateral clypeal carinae absent; occipital ridge nearly effaced; metasternum, along inner margin of each mesocoxa, with a single row of irregularly placed large punctures; elytral striae distinct, usually strongly punctate; last abdominal spiracle intrasternal; color metallic blue or green; length 12-15mm ..... *Mioxysternon*

– Cephalic process of male horn-like, often massive or, in small individuals, reduced to a pair of closely set median tubercles; that of female a strong, trituberculate carina; clypeal process transverse or spiniform; lateral clypeal carinae present, at least partially; occipital ridge strongly developed; metasternum not strongly punctate adjacent to mesocoxae; elytral striae present but often nearly effaced, never strongly punctate; last abdominal spiracle marginal; color variable, usually bright; length 10-35mm. .... *Oxysternon, sen. str.* 2

2. Dorsal surface of clypeus black; clypeal process spiniform; vertical, postero-lateral portion of circumnotal ridge effaced by a broad, oblique thickening (Fig. 211, arrow); each mesocoxa paralleled along outer side by wide, raised ridge-like portion of metasternum

MAP 3. Approximate distributions of the subgenera of *Oxysternon*. (?'s refer to occurrence of *Oxysternon, sen. str.*)

which does not bend dorsally at anterior end; front tibiae tridentate, only apical two teeth carinate on anterior surface; hind tibiae each with weak transverse carina on outer face near apex; hind apical tibial spur truncate distally ..... *festivum* group

– Dorsal surface of clypeus at least partially metallic; clypeal process transverse (spiniform in *palaemon*); circumnotal ridge not effaced postero-laterally; thickened outer border of mesocoxal depression narrow, bent dorsally at anterior end; front tibiae quadridentate, apical three teeth carinate anteriorly, basal tooth small; hind tibiae not carinate on outer apical surface; hind tibial spur acute .... *silenum* group

Subgenus **Oxysternon** Castlenau, *sensu stricto*

Oxysternon Castlenau, 1840: 82. Type: *Scarabaeus festivus* L., present designation.
Sternaspis Hope, 1837: 52 (junior homonym of *Sternaspis* Otto. Type: *Scarabaeus festivus* L., present designation.
Strombodes Gistel, 1857: 602. Type: *Scarabaeus festivus* L., original designation.

Among the members of this subgenus are the better known *Oxysternon*. All are large, usually conspicuously colored South American phanaeines (Map 3). Both constituent species groups are quite cohesive, although *palaemon* is a phenetic annectant between them (see below).

THE *festivum* GROUP (*festivum* [L.]; *macleayi* Nev.; *lautum* [MacL.]; *conspicillatum* [Web.]; *ebeninum* Nev.): Various structural details (particularly the shape of the pronota of well-developed males) can be used to subgroup the constituents of this taxon. Thus, *festivum* and *macleayi* form a species pair, and the remaining three species constitute a second subgroup. All species have characteristic coloration, which evidently varies little. Two, *festivum* and *conspicillatum*, are quite common in collections. Surprisingly little is known of the biology of this group, although collection data indicate all are amazonian. The range of *conspicillatum* is enormous, covering the entire Amazon Basin south of the Amazon and Rio Negro and certain non-basin areas (e.g., Quito, Ecuador). *O. festivum* is also amazonian but occurs north of the Amazon River (? into the Guianas); *festivum* has been collected from traps baited with human feces. The known range of *ebeninum* is restricted along the upper Rio Negro. Both *lautum* and *macleayi* are known only from the Amazon Basin.

THE *silenum* GROUP (*silenum* Cast.; *smaragdinum* Ols.; *sericeum* Ols.; *palaemon* Cast.): The most common species, *palaemon*, is noteworthy in that it shows features (e.g., spiniform clypeal process) otherwise unique to the *festivum* group. This species is coprophagous and occurs in great numbers in the savanna regions ("cerrados") of south-central Brazil. I have seen very few specimens of *silenum*, *smaragdinum* and *sericeum;* they appear so similar to me as to suggest conspecificity. All specimens of these three species that I have seen were collected at scattered localities in the western portions of the Amazon Basin.

Unassigned names probably *Oxysternon, sen. str.: biimpressum* Ols., *aeneum* Ols.

Mioxysternon *new subgenus*

Type: *Oxysternon spiniferum* Cast. (Derivation of subgeneric name: *mios* (dwarf) + *Oxysternon*, neuter; reference to relatively small size.)

This subgenus brings together three small-sized, rare species of *Oxysternon* (*spiniferum* Cast.; *curvispinum* Ols.; *pteroderum* Nev.) clearly distinguished from their congeners by those features mentioned in the key.

Most noteworthy of these are the apparent lack of a corniform cephalic process on otherwise well developed males, small size, obliteration of the occipital ridge and shape of the pronotum of the male (Figs. 214-215), which in the type-species resembles that of *Phanaeus bispinus*. The pronotum of the single male *pteroderum* I have seen bears two parallel, longitudinal crests rather than the parallel prolongations of *spiniferum*. Of interest is the fact that the cephalic process of the male of *Mioxysternon* resembles that characteristic of the "minor" males of *Oxysternon, sen. str.*, two closely-set tubercles. I have seen very few specimens of these species, all from scattered South American localities (Map 3).

Judging by original description, *striatopunctatum* Ols. would also fall in this subgenus.

Genus **Coprophanaeus** Olsoufieff

DESCRIPTION

(1) *anterior margin of clypeus emarginate medially* (Figs. 83-88); (2) *clypeal process U-shaped* (Fig. 114); lateral clypeal carinae present; (3) cephalic process of male corniform or lamellate (Figs. 181, 186, 188, 192-193); (4) cephalic process of female corniform (Fig. 182) or carinate; (5) paraocular areas of parietals usually narrow (Fig. 116); (6) postocular lobes of parietal depressed transversely, pronotal margin entire (Fig. 116) or weakly effaced but never distinctly broken by emarginations; canthal area usually distinct (Fig. 116A); (7) cephalic brachium monopodal (Fig. 126); (8) *eyes almost always large;* (9) *occipital ridge incomplete;* (10) *labrum* Coprophanaeus-*type* (Figs. 146-148); (11) *mentum weakly emarginate* (Fig. 157); (12) median lobe of hypopharynx present; (13) premental sclerites marginally sclerotized (as in Fig. 150); (14) pronotum of male type C, E or F (Figs. 181, 183, 186, 189, 192); (15) pronotum of female type A (Figs. 184-185, 190-191) or like type E of male (Figs. 181-182); (16) pronotum usually at least partially rugose or distinctly ridged (Fig. 166); posterior pronotal fossae usually present; (17) front tarsi present or absent in female; (18) *front tibiae* Coprophanaeus-*type* (Fig. 246); (19) middle and hind tarsi five-segmented; (20) sculpturing of elytral interstriae variable, usually smooth; (21) interstriae flat or convex; (22) striae sometimes carinulate; hind wing sometimes notched basally (Fig. 292); position of last abdominal spiracle variable.

This genus brings together three of the five subgenera of *Phanaeus* established by Olsoufieff (1924): *Coprophanaeus, Megaphanaeus* and *Metallophanaeus*. The subgeneric rank of these three taxa is here maintained. All *Coprophanaeus* are immediately recognizable by the presence of emarginate clypeus, strongly quadridentate front tibiae and usually distinct ridging of

the pronotum. The only other phanaeines likely to be confused with this genus are the few robust species of *Dendropaemon*. *Coprophanaeus* is South American although a few species occur in Mexico (Maps 4 and 5); all species whose habits have been observed are exclusively or ordinarily necrophagous, usually nocturnal and tend to occur in forests.

KEY TO THE SUBGENERA AND SPECIES GROUPS OF **Coprophanaeus**

1. Front tarsi present in female; striae conspicuous, always distinctly carinulate, carinulae straight or undulate (Fig. 288); hind wing not notched basally; last abdominal spiracle located within sternum 7 (though not visible laterally in *bellicosus*); posterior surface of each front tibial tooth with oblique, conspicuous brush-like clump of short setae; female cephalic process (except of *bellicosus*) and pronotal shape very similar to those of male such that sexual dimorphism, especially among smaller individuals, is not pronounced; pronotum of both sexes with an often massive, more-or-less saddle-shaped or quadrate process extending anteriorly from posterior portion of large median concavity; paraocular areas of parietals dorsally distinctly carinate lateral to eye; occipital areas of parietals each with angulate prominence; size large to very large (40-60mm); dorsum dark metallic blue, green or deep violet ..... *Megaphanaeus*

– Front tarsi absent in female; striae often nearly effaced, at most only weakly carinulate in some individuals with green elytra; hind wing notched or not basally; last abdominal spiracle marginal or set in distinct notch in edge of sternum 7; posterior surface of front tibial teeth each with single, oblique row of setae; sexual dimorphism, as expressed by cephalic and pronotal processes, very pronounced or not; pronotum of female with shallow antero-median concavity bordered anteriorly by transverse, crest-like ridge; pronotum of male variable; paraocular areas of parietals with no distinct carina lateral to eye (except in *pertyi* and *pessoai*); occipital areas of parietals more-or-less flattened, without distinct angulate prominence; size moderate (20-40mm); color variable 2

2. Hind wing not notched basally; width of lower portion of each eye less than twice (usually about equal) width of adjacent oculogular space; cephalic process of male a simple, tapering "horn"; color of pronotum and usually also elytra metallic, shining ..... *Metallophanaeus*

– Hind wing distinctly notched basally, vein V_2 usually conspicuously hooked apically (Fig. 292); lower portion of eyes large, bulging, width of each more than twice width of adjacent oculogular space; cephalic process of male lamellate, as in Figures 192, 193 or 188, never a simple, tapering horn; dorsum usually black or dull blue-black with metallic areas restricted to margins of pronotum, etc., rarely nearly wholly metallic green above (*C. spitzi* and some specimens of *C. milon* and *pluto*) ..... *Coprophanaeus, sen. str.* 3

3. Anterior portion of circumnotal ridge not distinctly effaced behind

eyes; last abdominal spiracle marginal, not set in distinct notch in sternum; posterior margin of paraocular areas of parietals (seen dorsally) straight, not bending toward posterior angle of eye; pronotum of large males never with strongly produced, quadrate median process; cephalic process of larger males as in Figures 192-193, its sides distinctly convergent apically ..... *jasius* group

– Anterior portion of circumnotal ridge distinctly effaced behind eyes, gaps so produced each as wide or wider than adjacent portion of eye (as in Fig. 119C); last abdominal spiracle set in distinct notch in dorsal margin of sternum 7; posterior margin of paraocular areas seen dorsally) distinctly bent toward posterior angle of eye; pronotum of well-developed males with large quadrate median process (Figs. 186-187); cephalic process of male with sides parallel or divergent, usually plate-like with two or three apical tuberculate processes (Fig. 188) ..... *dardanus* group

Subgenus **Megaphanaeus** Olsoufieff

Megaphanaeus Olsoufieff, 1924: 23 (as a subgenus of *Phanaeus*). Type: *Scarabaeus lancifer* L., original designation.

This subgenus includes some of the largest known Scarabaeinae; the largest phanaeines, *C. ensifer* and *lancifer,* regularly exceed 50mm in length; only some species of *Heliocopris* are larger. Also noteworthy is the strong resemblance of males and females in development of secondary sexual features, the most unusual aspect of which is the presence of a massive cephalic "horn" on the female. The sexual resemblance is only superficial since separation of sexes can always be immediately accomplished by examination for front tarsi, which are present only in females.

The name *Megaphanaeus* is used here as established by Olsoufieff. It includes four species (*lancifer* [L.]; *ensifer* Germ.; *bonariensis* Gory; *bellicosus* Oliv.), the first three of which are evidently rather closely related. These three species have strongly sculptured elytra with undulate strial carinulae; the pronotum is likewise strongly sculptured, bearing flattened granules which coalesce to form extensive transverse ridging. *C. bellicosus* differs from them in several respects: non-corniform cephalic process of the female (which closely resembles that of *Sulcophanaeus carnifex,* Figs. 201-202), smooth, flat elytral interstriae, straight elytral carinulae and deep violet color. (The above species are bright metallic blue, green or blue-green.) Among other features, elytral sculpturing can be used to separate the species of this subgenus.

With the possible exception of *bellicosus,* whose habits I do not know, *Megaphanaeus* is a necrophagous group. I have collected *lancifer* in surprisingly large numbers from carrion-baited traps along the Amazon River (Belém and Manaus) and *ensifer* in a similar manner in the state of São Paulo, Brazil. Martínez (1959) reports *bonariensis* to be necrophagous,

MAP 4. Approximate distributions of the subgenera *Megaphanaeus* and *Metallophanaeus*.

preferring bird carcasses. All species are South American (Map 4), where they appear to be restricted to forests.

Subgenus **Metallophanaeus** Olsoufieff

Metallophanaeus Olsoufieff, 1924: 22 (as subgenus of *Phanaeus*). Type: *Phanaeus saphirinus* Sturm, original designation.

This subgenus brings together two species-pairs, *saphirinus* Sturm-*hortus* (Waterhouse) and *pertyi* Ols.-*pessoai* Pereira. According to Martínez and Pereira (1967), *thalassinus* Perty, which I have not seen, is closely re-

lated to the latter pair. Both pairs are quite distinct and perhaps brought together only artificially here, the only alternative (which I consider inadequate) being to erect a separate subgenus for *pertyi-pessoai*. Olsoufieff (1924) and Martínez and Pereira (1967) include the latter pair in *Coprophanaeus, sen. str.* The general appearance of the *pertyi* group suggests an annectant taxon between *Metallophanaeus* and *Coprophanaeus, sen. str.* All species except *pertyi* occur in southern South America (Map 4); *pertyi* is limited to the arid regions ("caatinga") of northeast Brazil. Contrary to Halffter and Matthews (1966:30) *saphirinus* is at least sometimes necrophagous (Edmonds, 1967); the same authors cite *horus* as necrophagous.

Subgenus **Coprophanaeus** Olsoufieff, *sensu stricto*

Coprophanaeus Olsoufieff, 1924: 22 (as subgenus of *Phanaeus*). Type: *Scarabaeus jasius* Oliver, original designation.

The name *Coprophanaeus* is used here in a somewhat more restricted taxonomic sense than by Olsoufieff. The included species, which comprise the bulk of the genus, are all somber colored and robust and at a glance rather closely resemble each other.

THE *jasius* GROUP includes at least four species (*jasius* [Oliver]; *cerberus* [Har.]; *parvulus* [Ols.]; *spitzi* [Pessoa]) all restricted to South America (Map 5); *jasius* occupies an enormous range coincident with all but the southernmost regions of the composite range of the group. I have collected all four included species from carrion-baited traps in Brazilian forests.

THE *dardanus* GROUP also comprises at least four species (*milon* [Blanch.]; *telamon* [Er.]; *dardanus* [MacL.]; *pluto* [Har.]). The composite range of this group is much wider than the former. This is the only coprophanaeine taxon species of which occur outside South America; i.e., the Central American distribution indicated in Map 5.

Unassigned names probably belonging in *Coprophanaeus, sen. str.*: *costatus* Ols., *arrowi* Ols., *jasion* Fels., *boucardi* Nev., *punctatus* Ols., *conocephalus* Ols., *ohausi* Fels., *sericeus* Fels., *rex* Balths., *strandi* Balths., *roubali* Balths.

Genus **Dendropaemon** Perty

DESCRIPTION

(1) *anterior margin of clypeus emarginate medially* (Figs. 89-94, 132, 134); (2) *clypeal process U-shaped, sometimes reduced;* lateral clypeal carinate present or absent; (3) cephalic process of male usually carinate, sometimes lamellate (Fig. 305); (4) cephalic process of female carinate; *paraocular areas of parietals usually raised medially into large bump or transverse ridge* (Fig. 134); (5) *paraocular areas of parietals usually wide* (Fig. 134); (6) postocular lobes of parietals depressed transversely, circum-

MAP 5. Approximate distribution of *Coprophanaeus, sen. str.*

notal ridge not interrupted by emarginations (Figs. 123C, 124C); canthal area distinct (Figs. 123A, B, 124A, B); (7) cephalic brachium monopodal; (8) eyes small or large; (9) occipital ridge incomplete; (10) *labrum* Coprophanaeus-*type* (Figs. 144-145), *apical margin deeply emarginate, median brush reduced to few long setae inserting in apical fork of antero-median process of suspensorium;* (11) *mentum weakly emarginate* (Fig. 152); (12)

median lobe of hypopharynx absent; (13) premental sclerites marginally sclerotized (Fig. 151); (14-15) pronotum of both sexes usually similar, more-or-less ffattened (see discussion below); (16) pronotum partially roughened or entirely punctate; posterior pronotal fossae present; transverse propleural carina present (*Dendropaemon, sen. str.,* Figs. 179-180) or absent (*Coprophanaeoides* and *Paradendropaemon*); (17) front tarsi absent in female; (18) *front tibiae* Dendropaemon-*type* (Fig. 247) (except *ganglbaueri*); *lower apical angle of middle and hind femora expanded, covering base of tibia* (Figs. 268-269) (except *ganglbaueri*); (19) *middle and hind tarsi two- or three-segmented* (Figs. 270-279); (20) elytral interstriae smooth or punctate; (21) same evenly convex; (22) *striae carinulate* (Figs. 290-291) (very weakly so in *ganglbaueri*); hind wing notched (Figs. 294-295, 298) or not (Fig. 299); *base of pygidium impressed on each side of median furrow* (Fig. 162, ld) (very weakly so in *ganglbaueri*).

In addition to the above features, *Dendropaemon* is characterized by a remarkably great variation in body shape. Included in the genus are two species (*amyntas* and *ganglbaueri*) of the generally robust shape characteristic of other phanaeines (Figs. 304-305). Most *Dendropaemon,* however, are narrowed and dorso-ventrally flattened to some degree (Figs. 306-309). Following is a list of some of those observed skeletal features judged directly related to the flattening-narrowing trend among these species. As indicated, most vary continuously among progressively flatter, narrower species.

a. Reduction in size of cephalic process of male; prominent in robust species (Fig. 305), carinate in flattened species (Figs. 307, 309).

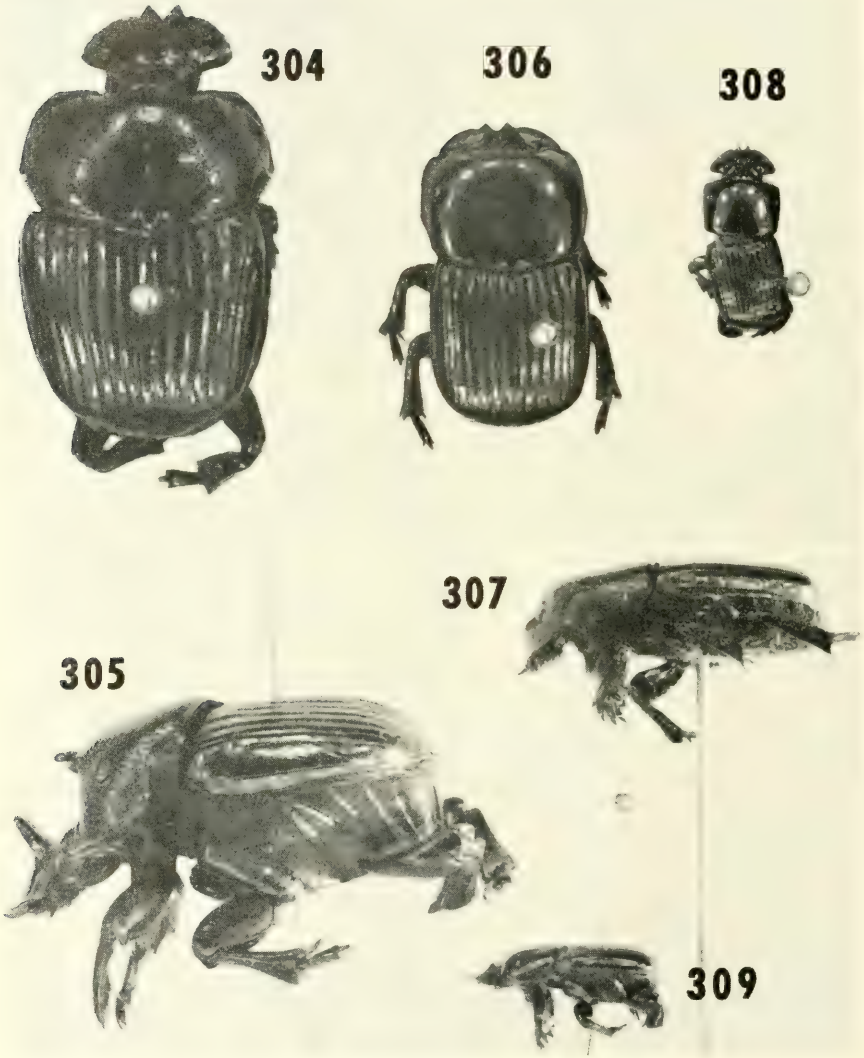
b. Dorso-ventral flattening of antennal club (Fig. 136A) in all species except *ganglbaueri;* in some (Fig. 136) flattening accompanied by elongation of first lamella (segment 7).

c. Maximal elongation of mentum, approximately as long as wide in all species (Fig. 152).

d. Progressive dorso-ventral flattening of prothorax, from robust (Figs. 167-168, 174) to successively more flattened (Figs. 170, 173, 175-176); flattening is accompanied by progressive narrowing and squaring of dorsal outline, from rounded laterally (Figs. 169, 304) to more parallel-sided (Figs. 171, 177, 306, 308) and by reduction of pronotal processes (cf., Figs. 167, 176).

e. Narrowing of mesoscutellum; in all *Dendropaemon* length at least equal to, but usually greater than width (Fig. 229); in other phanaeines, width always greater (usually much greater) than length (Fig. 44).

f. Flattening and elongation of metepisternum; in other phanaeines and in robust *Dendropaemon,* length (along dorsal margin) less than 1.5 times height (along anterior margin) (Figs. 54, 241, 244); in flattened species,



FIGS. **304-309. 304,** *Dendropaemon amyntas,* male, dorsal view; **305,** same, lateral view; **306,** *D. viridis,* male, dorsal view; **307,** same, lateral view; **308,** *D. nitidicollis,* male, dorsal view; **309,** same, lateral view.

length progressively proportionately greater, but always more than twice height (Figs. 232, 235, 238, 242-243).

g. Narrowing of metasternum; in robust species, length of its median area (from antero-median angle to posterior margin) only slightly greater (less than 1.25 times) than width (smallest distance between mesal margins

of coxal depressions) (Fig. 51); in narrowed species, length progressively proportionately greater but always twice or more width (Figs. 231, 234, 237); accompanying narrowing is progressive reduction in prominence of anteromedian angle of metasternum (Figs. 230, 233, 236).

h. Narrowing of elytra; in robust species, combined widths of elytra (at humeral angles) greater than length (along elytral suture) (Fig. 304); in narrowed species, length greater than width (Figs. 306, 308); narrowing accompanied by proportionate narrowing of abdomen, which is covered by elytra.

Primarily because of the great variation in general form it is difficult to recognize *Dendropaemon* immediately using superficial "sight" criteria. Most species are more-or-less flattened, elongate and parallel-sided; all have a reduced number of tarsomeres (two or three). The extreme of the elongation-flattening trend observable in smaller species of the genus is paralleled in *Onthocharis* Westwood which superficially resembles small *Dendropaemon* also in color (metallic green) and clypeal emargination, and in *Stiptopodius* Har.

A meaningful evolutionary interpretation of the remarkable variation in form of *Dendropaemon* is largely precluded by a lack of reliable data on its biology, which likely will prove to be quite aberrant. The genus name means "tree dweller," an appellation of doubtful accuracy. Olsoufieff (1924: 121) and Blut (1939:263) state emphatically that *Dendropaemon* inhabit rotting wood; Halffter and Matthews (1966:40) suggest they may feed on fungi in rotting wood. Blut (p. 266) goes so far as to say that given species of *Dendropaemon* feed selectively in given species of hardwood trees! Evidently, however, the wood-dwelling habits of the genus have yet to be positively demonstrated. All specimens about which I could learn circumstances of capture (from collector or label) were collected at lights or lying dead on the ground. Moreover, neither I nor any other collector whom I know personally has been able to collect adults from rotting logs, etc., in localities where they are known to occur. To my knowledge, *Dendropaemon* has likewise never been collected along with other phanaeines from carrion or feces of any kind. That some (or all) species could be dendrophilous is, of course, possible; but other, equally possible habitats have not yet been adequately explored, such as vertebrate burrows and nests, nests of ground-dwelling termites and ants, and fungi (particularly hymenomycetes).

Most museum specimens of *Dendropaemon* are quite old and, hence, apt to bear non-precise locality data. Consequently, Map 6 is at best a tenuous approximation of the range of the genus. The detailed distributional comments of Blut (1939:265) need confirmation.

A detailed revision of *Dendropaemon* species is greatly needed. The

MAP 6. Approximate distributions of *Megatharsis*, *Tetramereia* and *Dendropaemon*. (?'s refer to occurrence of *Dendropaemon*.)

descriptions and keys of Olsoufieff (1924), Pessoa and Lane (1936) and Blut (1939), which in general were based on too few specimens, need enlargement and clarification. Blut lists twenty-five species, fifteen of which I have examined in addition to two others of uncertain name. Heretofore the genus has been informally divided into two species groups based on number of tarsal segments (two or three). In the following treatment tarsomere number is de-emphasized since other, more reliable variation quite clearly indicates an altogether different systematic picture.

Key to the Subgenera and Species Groups of **Dendropaemon**

1. Abdominal sternum 7 long, as long as combined lengths of sterna 5 and 6 (Fig. 300); inner basal angle of front tibiae not expanded as in Figure 247, tibiae gradually narrowing basally; hind tarsi two-segmented, basal segment cylindrical, nearly as long as tibia, apical segment minute, hemispherical (Fig. 278, arrow indicates apical segment); color dull black-brown ..... *Paradendropaemon*
– Abdominal sternum 7 no longer (usually shorter) than sternum 6 alone; front tibiae as in Figure 247; hind tarsi two- or three-segmented, basal segment flattened, its length never approaching that of tibia; color variable 2
2. Transverse propleural carina absent; eyes large (Figs. 132-133); tarsi three-segmented (Fig. 274) ..... *Coprophanaeoides*
– Transverse propleural carina present (Figs. 179-180, arrows); eyes small (Fig. 134; large in *denticollis*); tarsi two- or three-segmented ..... *Dendropaemon, sen. str.* 3
3. Transverse propleural carina complete, extending laterally beyond coxa (Fig. 180); emarginations of anterior clypeal margin variable (Figs. 90, 92-93); tarsi three-segmented (Figs. 273, 275-276); hind wing not notched (Fig. 299); length 8-15mm ..... *viridipennis* group
– Transverse propleural carina incomplete, not extending laterally from coxa (Fig. 179); emarginations of clypeal margin as in Figures 94 and 134; tarsi two- or three-segmented; hind wing notched or not 4
4. Middle and lateral emarginations of clypeus rounded, teeth rounded (Fig. 94); tarsi three-segmented (Figs. 270-271; two-segmented in *smaragdinum*, Fig. 272); hind wing at most only slightly notched (Fig. 298); length 6-9mm; flattened, elongate, metallic green species ..... *denticollis* group
– Middle emargination of clypeus acute, lateral emarginations absent, teeth acute (Fig. 134); tarsi two-segmented (Fig. 277), length of basal segment more than three times length of apical segment; hind wing deeply notched (Fig. 295); length 7-12mm; flattened, solid black or metallic green species ..... *piceum* group

Paradendropaemon *new subgenus*

Type: *Dendropaemon ganglbaueri* Felsche. (Derivation of subgeneric name: *para* [beside] + *Dendropaemon*, neuter; reference to taxonomic isolation within genus.)

I have seen only one specimen of *Dendropaemon ganglbaueri* (a female), but it is so unlike its congeners that I must conclude that it warrants placement in a distinct subgenus. The following are those features which contribute to its uniqueness: (1) very large, triangular clypeal teeth (Fig. 91), (2) evenly tapering front tibiae (not strongly expanded basally as in other *Dendropaemon*, Fig. 247), (3) middle and hind femora not expanded apically as in other *Dendropaemon* (Figs. 268-269), (4) convex, evenly granulo-rugose pronotum (very similar to that of *Tetramereia* and *Homalotarsus*), (5) unique hind tarsi (Fig. 278), (6) exceptional length of ab-

dominal sternum 7 (Fig. 300), which is proportionately much greater than in any other phanaeine, and (7) only very weak, scarcely visible lateral depressions of base of the pygidium (distinctly strongly depressed in all other *Dendropaemon*). It is, of course, possible that any of the above features may be limited to the female. This robust species is known so far only from a few localities in the state of São Paulo, Brazil.

Coprophanaeoides *new subgenus*

Type: *Dendropaemon renatii* Olsoufieff. (Derivation of subgeneric name: *Coprophanaeus* + *-oides* [resembling], neuter; reference to resemblance to *Coprophanaeus, sen. str.*)

This subgenus brings together at least three species, the names of only two of which I can use confidently: *renatii* Ols. and *hirticollis* Ols. I have studied a third species under the name of *bahianum* Har., considered by Blut (1939: 295-296, *q.v.*) as of *incertae sedis* because of the confusion attending its original description and subsequent usage. These three species bear striking resemblance to *Coprophanaeus, sen. str.*, particularly because of the shape of the medial emargination of the clypeus (Fig. 132), large eyes (Figs. 132-133), ridged pronotal sculpturing and deeply emarginate hind wings. Unlike any other phanaeine, the entire upper surface of *hirticollis* is covered by scattered, erect setae. The distributional data that I have indicate that the range of *Coprophanaeoides* is centered in southern Brazil.

Subgenus **Dendropaemon** Perty, *sensu stricto*

Dendropaemon Perty, 1830: 30. Type: *Dendropaemon piceum* Perty, subsequent designation by Blut, 1939: 267.

Enicotarsus Castlenau, 1831: 35. Type: *Enicotarsus viridipennis* Cast., by monotypy.

Onthoecus Dejean, 1837: 156. Type: *Dendropaemon amyntas* Har., present designation.

The bulk of the species studied fall into this subgenus, the most salient feature of which is the presence of propleural carinae. The species included here express the entire range of body shape variation described above, the extremes of which are shown by *D. amyntas* (Figs. 304-305) and *D. nitidicollis* (Figs. 308-309).

THE *viridipennis* GROUP comprises four rather large (15-22mm) species bearing complete transverse propleural carinae and three-segmented tarsi (*viridipennis* [Cast.]; *amyntas* Har.; *fractipes* Felsche; *lobatum* Waterh.). *D. amyntas*, a robust species, superficially resembles "normal" phanaeines, and, besides *ganglbaueri*, it is the only *Dendropaemon* likely to be so confused. *D. lobatum* is a subcylindrical species which, although parallel-sided, presents cephalic and pronotal processes similar to those of *amyntas*. The other species, while large, are distinctly flattened and parallel-sided. *D. viridipennis* bears a striking resemblance to *viridis* in size, shape and color.

THE *denticollis* GROUP here includes five, very similar small (7-11mm) metallic green species (*denticollis* Felsche, *nitidicollis* Ols., *fasces* Blut,

haroldi Ols., *smaragdinum* Waterhouse). All have distinctly rounded clypeal teeth and emarginations (Fig. 94) and incomplete propleural carinae. *D. nitidicollis* (Figs. 308-309) is the smallest known phanaeine (length 7mm).

The *piceum* group comprises three species with incomplete propleural carinae, single emargination of clypeus with large, acute teeth (Figs. 90, 134) and two-segmented tarsi (Fig. 277). The hind wing of these species is distinctly deeply notched (Fig. 295) (*piceum* Perty, *telaphum* Waterhouse, *viridis* Perty).

Unassigned names probably *Dendropaemon sen. str.* (based on Blut, 1939): *reflugens* Waterhouse, *angustipennis,* Har., *silvanum* Blut, *batrachites* Blut, *similis* Blut, *subcylindricum* Blut, *tenuitarsis* Felsche, *crenatostriatum* Felsche, *quadratum* Cast.

Genus **Tetramereia** Klages

Tetramereia Klages, 1907: 141. Type: *Tetramereia frederickii* Klages = *Dendropaemon convexum* Har., original designation.

Eurypodea Klages, 1906: 1. Type: *Eurypodea fredericki* Klages = *Tetramereia frederickii* Klages = *Dendropaemon convexum* Har., by monotypy.

Boucomontius Olsoufieff, 1924: 120. Type: *Dendropaemon convexum* Har., by monotypy.

Tetramereia convexa (Har.) (Figs. 312-313) is a robust, brown species with an involved nomenclatorial history during which it has been placed in four genera (as type-species of three!). Klages (1906) proposed the name *Eurypodea fredericki (n. gen., n. sp.)* in a single page article printed at his own expense. A series of errors resulted in the publication of another description of the same species proposing the name *Tetramereia frederickii* (Klages, 1907). Both descriptions were based on the same specimen. Olsoufieff (1924: 120), suspecting the duplication, nevertheless proposed still another genus name, *Boucomontius,* for *Dendropaemon convexum* Har., later found to be a senior synonym of *T. frederickii.* I have elected for now to continue usage of the name *Tetramereia* for two reasons: 1) I have judged *Eurypodea* does not comply with Articles 7 and 8 (Chapter IV, Criteria of Publication) of the International Code of Zoological Nomenclature and, hence, is unavailable (Art. 10) (see also Janssens, 1940); 2) *Tetramereia* is the name now of common usage. Nevertheless, I have requested that the International Commission on Zoological Nomenclature render an opinion on the availability of the name *Eurypodea.*

DESCRIPTION

(1) *anterior margin of clypeus not emarginate medially, distinctly toothed* (Fig. 95); (2) clypeal process reduced, a small, very weak transverse ridge; lateral clypeal carinae absent; (3-4) *cephalic process of both sexes a simple transverse carina;* paraocular areas of parietals flat and (5) wide; (6) postocular lobes of parietals depressed transversely, anterior portion of circum-

notal ridge not interrupted by emarginations; canthal area distinct; (7) cephalic brachium monopodal; (8) eyes small; (9) occipital ridge incomplete; (10) labrum resembling *Coprophanaeus*-type (Figs. 142-143); (11) *mentum weakly emarginate* (Fig. 153); (12) median lobe of hypopharynx absent; (13) premental sclerites marginally sclerotized; (14-15) *pronotum of both sexes evenly convex* except for small, antero-median transverse carina; (16) pronotum evenly granulo-rugose; posterior pronotal fossae absent; mesometasternal suture angulate (as in Fig. 240); mesoscutellum as long as wide (as in Fig. 239); (17) front tarsi absent in female; (18) front tibiae quadridentate, apical three teeth carinate (Fig. 249); (19) *middle and hind tarsi four-segmented* (Fig. 263); (20) elytral interstriae weakly punctured, (21) evenly convex; (22) striae simple; hind wing not notched (Fig. 297); last abdominal spiracle marginal; length 13-15 mm.

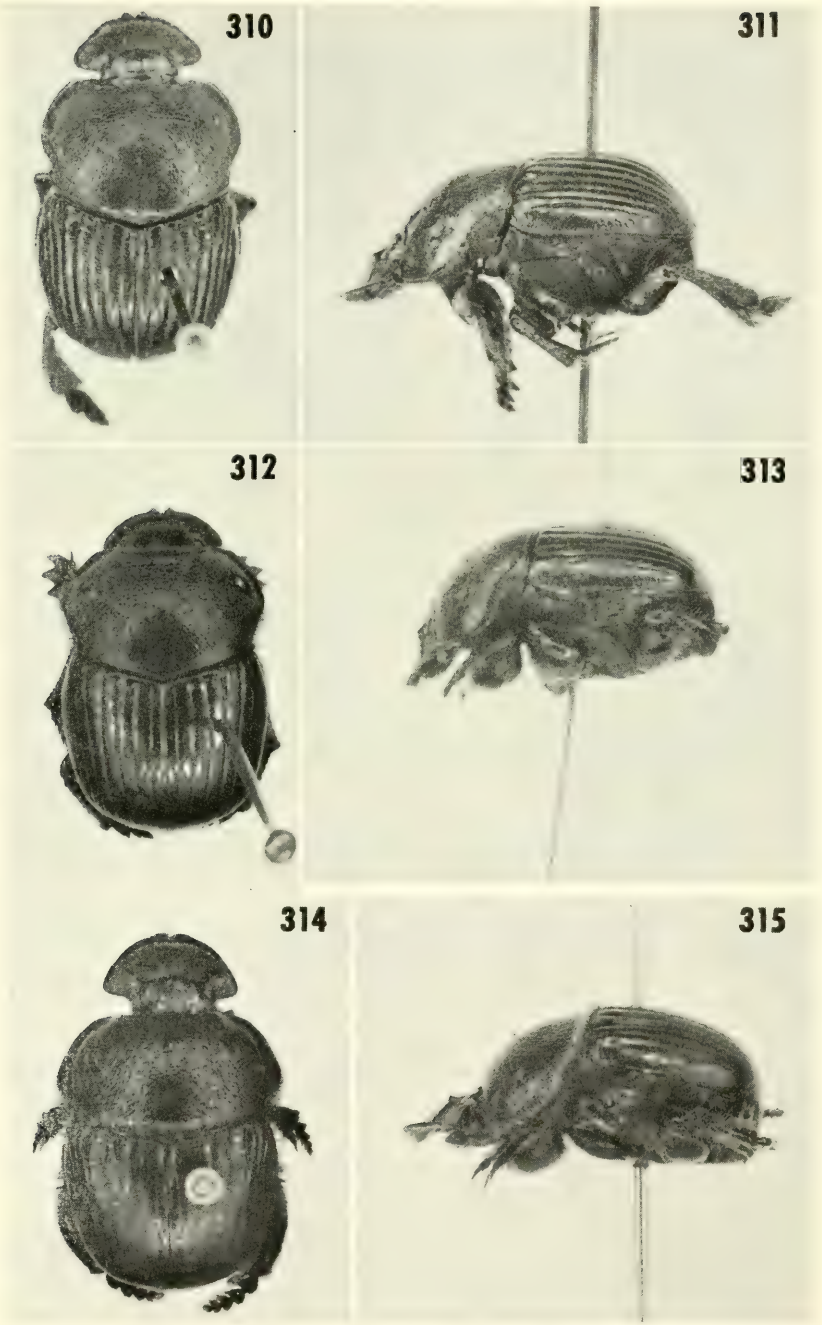
So far this species is known only from a few scattered South American localities (Map 6); the type locality of *frederickii* is Suapure, Cuara (River) Valley, Venezuela. *Tetramereia convexa* very closely resembles *Homalotarsus impressus* (see discussion of *Homalotarsus* below). It is the only known phanaeine with four-segmented tarsi, a feature which indicated to Blut (1939) and Olsoufieff (1924) an intermediate phylogenetic position of the genus between *Dendropaemon* and *Megatharsis* (see phylogenetic discussion in the last part of this paper). Because of the lack of developed cephalic and pronotal protuberances, the sexes of this species very closely resemble each other. The biology of *Tetramereia* is unknown.

Genus **Homalotarsus** Janssens

Homalotarsus Janssens, 1932: 119. Type: *Homalotarsus impressus* Janssens (by original designation and monotypy).

To my knowledge only two specimens of this curious phanaeine are known, both of which are deposited in the Institut Royal des Sciences Naturelles de Belgique (Brussels). The holotype is labeled "South America"; the second specimen, "Brazil." I was able to examine only the latter (sex unknown; Figs. 310-311); it bears Janssens' determination label and agrees with his original description of the genus. *Homalotarsus impressus* is remarkably similar to *Tetramereia convexa,* and the two should likely be considered congeners. Nevertheless, until more is known about both species, I choose to maintain the generic distinction.

I was unable to examine the mouthparts and endoskeletal features of *H. impressus;* I have assumed that they are similar to their counterparts in *Tetramereia.* Moreover, because of their great similarity, I have restricted my description of *Homalotarsus* to the following observed features which differ markedly from their counterparts in *Tetramereia;* those features not mentioned are as in *T. convexa* (see above):



FIGS. **310-315.** **310,** *Homalotarsus impressus,* female?, dorsal view; **311,** same, lateral view; **312,** *Tetramereia convexa,* female, dorsal view; **313,** same, lateral view; **314,** *Megatharsis buckleyi,* female, dorsal view; **315,** same, lateral view.

1. shape of mentum and labial palpi as in Figure 156;
2. shape of front tibia as in Figure 254, apical tooth not carinate;
3. middle and hind tarsi five-segmented (Figs. 264-265);
4. dorsal surface of apex of hind femur, of tibia and of first four tarsomeres bearing large setigerous granules (Fig. 260);
5. color metallic yellow-green.

Genus **Megatharsis** Waterhouse

Megatharsis Waterhouse, 1891: 59. Type: *Megatharsis buckleyi* Waterhouse, by monotypy.

Although Waterhouse (1891) likened this species to *Bolbites onitoides* Har., *Megatharsis buckleyi* (Figs. 314-315) is a unique phanaeine which, to my eye, resembles *Bolbites* very little if at all. I have examined only two specimens (females), both collected in Macas, Ecuador; the type locality is nearby Chiquinda, Ecuador (Map 6). The following description is based on females although I fully expect the male to agree closely with it; Waterhouse failed to mention the sex of the holotype.

DESCRIPTION

(1) anterior margin of clypeus not emarginate medially, obtusely bidentate (Figs. 96, 135); (2) clypeal process reduced to small gibbosity; lateral clypeal carinae present; (4) cephalic process of female (and male?) a transverse, trituberculate carina (Fig. 135); paraocular areas of parietals flat, (5) wide; (6) postocular lobes of parietals depressed transversely, anterior portion of circumnotal ridge not emarginate; canthal area distinct, small; (7) cephalic brachium monopodal; (8) eyes small; (9) occipital ridge incomplete; (10) labrum resembling *Coprophanaeus*-type (Figs. 140-141); (11) mentum weakly emarginate (Fig. 154); (12) median lobe of hypopharynx absent; *labial palpi of one segment* (Fig. 154) *with membranous slit on dorsal surface* (Fig. 155, arrow); (13) premental sclerites marginally sclerotized; (15) pronotum of female (and male?) evenly convex, (16) evenly granulo-rugose and *margined posteriorly by fringe of long setae behind a sharp, transverse carina* (Fig. 178); posterior pronotal fossae absent; mesometasternal suture angulate medially (as in Fig. 240); (17) front tarsi absent in female; (18) front tibiae quadridentate (Fig. 248); (19) middle and hind tarsi five-segmented, *segments of characteristic shape* (Figs. 266-267); *dorsal surface of hind tibiae with dense, longitudinal fringe of hair* (Fig. 266); (20) elytral interstriae punctate, (21) weakly convex, nearly flat; (22) striae simple; hind wing not notched (Fig. 296); last abdominal spiracle marginal; *abdominal sterna 3-7 each produced as small acute tooth projecting from beneath elytral margin; abdominal sterna 3-7 with dense fringes of long hair, completely traversing sternum 7* (Fig. 301) *while restricted laterally on sterna 3-6;* length 10mm; color dull blue or green.

PART VI: EVOLUTION AND PHYLOGENY OF PHANAEINES

Fossil phanaeines are unknown. Frenguelli (1938, 1939) attributed to *Phanaeus* ("o un género afin") brood balls recovered from various Tertiary deposits (Oligocene through Pleistocene) in southern Argentina.[12] Pierce (1946), describing *Palaeocopris* from the La Brea tar pits (Los Angeles, California; Pleistocene), suggests a morphological resemblance to this genus with *Phanaeus;* I have not seen the type material of *Palaeocopris.*

Lacking meaningful paleontological data, systematists concerned with evolutionary and phylogenetic questions are forced to base conclusions upon neontological data. The purpose of this discussion is to consider (1) the phylogenetic (cladistic) relationships among phanaeines indicated by an evolutionary interpretation of the comparative skeletal morphology and the biology of contemporary forms, and (2) the evolutionary implications of the ecology and distribution extant phanaeines.

Some Preliminary Considerations

Data for this discussion are essentially the same available for any approach to inferences about relationships, whether intended to be strictly phenetic or strictly cladistic. Since the data are the same, the conclusions of phenetic vs. phylogenetic inferences about relationships differ only as a result of the way they are treated. The evolutionary and phylogenetic conclusions arrived at here are based upon phenetic relationships indicated primarily by morphological characters and upon presumed cladistic relationships inferred by stressing (weighting) certain characters and by making judgments about evolutionary direction.

Phylogenetic speculation requires some *a priori* notions about evolutionary direction; that is, it requires decisions about which state of a character employed in assessing relationships is "primitive" (has undergone little or no evolution since the origin of a group; = plesiomorphous character of Hennig, 1965, 1966) and which is (are) "derived" (= "modified" = "specialized"; apomorphous character of Hennig). Table 1 lists for phanaeines the presumed primitive and derived states for some of the characters used in this study which lend themselves to such judgment. Table 1 is, in effect, a list of evolutionary trends observable in phanaeines. It is to be noted, however, that while certain character states are designated as primitive for phanaeines (e.g., striking sexual dimorphism, metallic color), they may be specialized ones when considering Scarabaeinae as a whole. In these instances, the derived state in phanaeines can be a secondary (convergent) condition and phenetic equivalent of the primitive state for the entire subfamily. An im-

[12] Gonzalo Halffter (pers. comm.) has examined the brood balls used in Frenguelli's studies and concludes that they are essentially of the type presumed characteristic of phanaeines and isolated species of *Dichotomius* (see Halffter and Matthews, 1966:130-139).

TABLE 1. Primitive and derived features of phanaeines.

Character*	Primitive State	Derived State(s)
1. Shape of anterior margin of clypeus	Not emarginate medially	Emarginate medially
2. Shape of clypeal process	Transverse	Spiniform, U-shaped or reduced
A Lateral clypeal carinae	Present	Absent
3. Shape of cephalic process of male	Corniform	Lamellate, carinate
4. Shape of cephalic process of female	Carinate	Corniform
5. Width of paraocular areas	Narrow	Wide
6. Shape of postocular lobes of parietals—anterior portion of circumnotal ridge	Depressed transversely—not emarginate	Depressed obliquely—emarginate
7. Shape of cephalic brachium	Monopodal	Bipodal
8. Size of eyes	Small	Large
9. Occipital ridge	Incomplete	Complete
10. Type of labrum	*Phanaeus*-type	*Coprophanaeus*-type
11. Shape of mentum	Strongly emarginate	Weakly emarginate
12. Median lobe of hypopharynx	Present	Absent
13. Premental sclerites	Marginally sclerotized	Completely sclerotized
16. Pronotal sculpturing	Smooth-punctate	Roughened
17. Front tarsi of female	Present	Absent
18. Front tibiae	*Phanaeus*-type	*Coprophanaeus*-type *Dendropaemon*-type
19. Middle and hind tarsi	Five segmented	With fewer than five segments
22. Striae	Simple	Carinulate
B Hind wing	Not notched basally	Notched basally
C Position of last abdominal spiracle	Marginal	Intermediate, intrasternal
D Color	Bright (metallic)	Sombre
E Size	Length under 30 mm	Length over 30 mm
F Secondary sexual dimorphism**	Striking (sexes very different)	Subtle (sexes similar)
G Feeding habit	Coprophagous	Necrophagous
H Time of activity	Diurnal	Nocturnal

* Numbering of characters corresponds to that in part III: reference should be made to this part for complete definition of morphological character states and their taxonomic distribution. Those characters designated A-H are characters either discussed, but not numbered, in part III or not discussed in that part.

** Based principally upon cephalic and pronotal shapes of well developed individuals.

portant group of characters is not included in Table 1: those which, because of their restricted taxonomic occurrence, are considered phanaeine specializations (e.g., transverse clypeal carina of *Diabroctis,* the several unique features of *Dendropaemon* and its subtaxa, etc.). These specializations, which are obviously most useful in "keying" the taxa to which they are restricted, are taken into account in the following discussions.

The direction of evolution is sometimes intuitively self-evident. Thus, a tarsal complement of fewer than five segments in phanaeines (and other

dung beetles) can (to me) be construed only as arising from the loss (or fusion) of one or more segments. In many instances, however, logical decisions depend largely upon a knowledge of variation in non-phanaeine taxa; for this reason it was necessary to examine other, non-phanaeine dung beetles (see Appendix for a list of those examined). When highly subjective judgments were called for in Table 1, the following points were considered: Since evolution as it is now understood tends to be a conservative process, a character state of widespread occurrence among otherwise quite diverse taxa is probably a primitive one. Accordingly, in character 7 the designation of a monopodal brachium as primitive was based principally upon the presence of monopodal brachia in all non-phanaeine scarabaeines examined as well as in the majority of phanaeines. Furthermore, the evolutionary status of the morphological character states regarded as correlates of behavorial trends are most logically considered the same as the status of the behavioral phenomena in question. Thus, if necrophagy in phanaeines is a specialized behavioral pattern, character states regarded as morphological correlates of necrophagy (e.g., emarginate clypeus) are no doubt also derived.

In making phylogenetic inferences I have stressed a fundamental hypothesis of "phylogenetic systematics" as most comprehensively approached by Hennig (1965, 1966): that, *when practical,* taxa should be recognized on the basis of shared derived character states, i.e., by synapomorphy or joint possession of apomorphous features (Hennig), since to do so increases the probability that taxa recognized are monophyletic. I do not, however, consider myself a phylogenetic systematist in the rigid sense of Hennig since I have chosen to temper the process of classifying and subsequent ranking of taxa with some measure of "taxonomic practicality." A "true" phylogenetic systematist (if such a person exists) might object to the phrase, "when practical," above. Thus, the classification of phanaeines proposed above does not completely reflect my ideas about the phylogenetic relationships among phanaeines, which are discussed below.

Phylogenetic Speculation

Table 2 shows the taxonomic distribution of the character states of the 26 characters listed in Table 1. For each taxon listed in Table 2 the per cent frequency of derived states (%D) is given at the right.[13] Using these percentage figures it is possible to generalize about the *relative* overall "primitiveness" (or "derivedness") of the various taxa based on those 26 characters. Thus, taxa 3 and 4, the *auricollis* and *imperator* groups of *Sulcophanaeus,*

[13] In calculating %D, "O" entries were counted twice, once as primitive, once as derived; "X" entries were disregarded. Ordinarily %D = no. D's/26; but for, say, *Oxysternon, sen. str.,*

$$\%D = \frac{\text{no. dots} + \text{no. O's}}{26 + \text{no. O's} - \text{no. X's}} \times 100\%.$$

TABLE 2. Taxonomic distribution of the states of 26 characters. Solid dot = derived state (different sizes indicate different derived states for same character); O = equal frequency of primitive and derived states among constituent species of indicated taxon; X = not known or not comparable; no symbol = primitive state. See text for further details.

Taxon \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	16	17	18	19	22	A	B	C	D	E	F	G	H	% D
1. Diabroctis			●																				●	●			12
Sulcophanaeus																											
2. faunus grp				●			O							O							O	O	●	●			23
3. imperator grp							O																				4
4. auricollis grp																						O					4
Oxysternon																											
5. Oxysternon, s. s.		O				X	●		●				●										O				19
6. Mioxysternon		●	●			X	●		●				●						●		●						28
Phanaeus																											
7. splendidulus grp						●	●		●				●														15
8. vindex grp						●	●		●				●	●													19
Coprophanaeus																											
9. Megaphanaeus	●	●		●				●		●	●			●		●		●			●		●	●	●	●	54
10. Metallophanaeus	●	●								●	●			●	●	●									●	●	35
11. Coprophanaeus, s. s.	●	●	●					●		●	●			●	●	●				●		●	O	O	●	●	54
Dendropaemon																											
12. Dendropaemon, s. s.	●	●	●		●					●	●	●		●	●	●	●	●		O				●	X	X	56
13. Paradendropaemon	●	●	●		●					●	●	●		●	●		●					●		●	X	X	50
14. Coprophanaeoides	●	●	●		●			●		●	●	●		●	●	●	●	●		●				●	X	X	63
15. Megatharsis		●	●		●					X	●	●		●	●				●					●	X	X	39
16. Tetramereia		●	●		●					X	●	●		●	●		●		●			●		●	X	X	48
17. Homalotarsus		●	●		●					X	●	●		●	●				●					●	X	X	39

emerge as most primitive (%D = 4), hence most obvious choices as the closest phenetic (and phyletic) approaches to "palaeophanaeines," while *Dendropaemon* (average %D = 58) appears to be the most highly evolved, hence most different from some hypothetical common ancestor.

Table 2 is somewhat misleading since some groups (particularly taxa 12-17) can actually be considered more highly evolved relative to the others than indicated by %D's. This is so since most of those character states unique to these taxa and, therefore, considered derived, are not enumerated *per se* in Tables 1 and 2. The incidence of such unique characters is especially high in *Dendropaemon* (e.g., body shape variation, lateral depression of base of pygidium, forked antero-median process of labral suspensorium, reduction in number of setae comprising median brush, etc.; see systematic section). The incorporation of these characters into Table 2 in the case of *Dendropaemon* and other taxa would only intensify the phenetic gaps indicated there; the relative positions of all taxa on an "evolutionary scale" would not change. Incidence of "concealed synapomorphy" will be discussed more fully below.

Of the 26 characters listed in Table 2, I have judged some intrinsically more useful than others for purposes of deducing phylogenetic relationships. Those presumed high in phyletic information content are shaded in Table 2. Those characters not shaded (omitted from phylogenetic considerations) form two principal groups: (1) some characters (12, 17, 19, A) were excluded because they are regressive, that is, their evolution involves loss or "reduction" (character 2, which is partially regressive, was not altogether ignored). I have accepted the hypothesis that regressive features (character states) are inherently more susceptible than progressive ones to parallel or convergent development (see, for example, Mayr, 1969: 222-223). Summary exclusion of regressive characters has probably resulted here in little loss of phyletic information since their inclusion would not significantly alter my phylogenetic inferences about phanaeines. (See discussion of parallelisms below.) (2) Characters D-H were excluded for discretionary reasons. Separation of largely discrete states of characters D, E and F is highly subjective; the designation of primitive states of characters G and H is based on unequal knowledge (e.g., the feeding habits of relatively very few *Sulcophanaeus* are known, but these are coprophagous; on the other hand, relatively a large number of *Phanaeus* are known to be coprophagous; as indicated by available, but unequally representative data, I assume both groups to be basically coprophagous).

Taxonomic data on the phylogenetic (shaded) characters in Table 2 have been reorganized in Table 3 as a phyletic "affinity matrix" showing the frequency of shared *derived* character states (= frequency of synapomorphy) between all possible pairs of taxa. One can observe directly in Table 3 pat-

TABLE 3. Affinity matrix (taxon X taxon) based on frequency of shared derived character states (synapomorphy) among pairs of phanaeine taxa. Taxa are numbered as in Table 2.

Taxa																
1	–	*Diabroctis*														
2	0	–														
3	0	1	–	*Sulcophanaeus*												
4	0	0	0	–												
5	0	1	1	0	–											
					Oxysternon											
6	1	2	1	0	3	–										
7	0	1	1	0	3	3	–									
							Phanaeus									
8	0	2	1	0	3	3	4	–								
9	0	3	0	0	0	1	0	1	–							
10	0	1	0	0	0	0	0	1	6	–	*Coprophanaeus*					
11	1	1	0	0	0	1	0	1	7	6	–					
12	1	1	0	0	0	1	0	1	6	5	7	–				
13	1	1	0	0	0	1	0	1	5	5	6	7	–	*Dendropaemon*		
14	1	1	0	0	0	1	0	1	7	5	8	10	7	–		
15	1	1	0	0	0	1	0	1	2	2	3	4	4	4	–	*Megatharsis*
16	1	1	0	0	0	1	0	1	2	2	3	4	4	4	4	– *Tetramereia*
17	1	1	0	0	0	1	0	1	2	2	3	4	4	4	4	4 – *Homalotarsus*
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16 17
	Taxa															

terns of high and low frequency of synapomorphy between, among and within genera. All taxa (1-17) are presumed monophyletic, the constituent species (one or more) of which are themselves related by synapomorphous states described fully only in the classification proposed above. Open triangles along the diagonal in Table 3 embrace *intra*generic comparisons for those genera with two or more subgeneric groupings.

If, as is assumed, frequency of synapomorphy is a valid measure of inferred phyletic (cladistic) relationship, one should expect the relative fre-

quency of synapomorphy to complement the classification of the groups for which comparisons are made. That is, in the case of phanaeine taxa, one should expect (where applicable) the *intra*generic frequency of synapomorphy to be greater than *inter*generic frequency, and that groups thus defined should be assignable to hierarchical groups largely corresponding with those of the classification proposed above. With some significant exceptions to be discussed below, this seems to be the general case. Inspection of Table 3 reveals two rather distinct phyletic generic groupings and two enigmatic groupings together with some inferences about evolutionary rates. Phylogenetic "conclusions" are presented below under two headings, generic affinities and parallelisms, and summarized in Figures 316 and 317.

Generic Affinities

Genus-group 1: *Phanaeus-Oxysternon*. A relatively close phyletic relationship between these genera is characterized by the presumed evolutionary fixation of three derived features, the first two being unique to the genus group: a complete occipital ridge, completely sclerotized premental sclerites and bipodal cephalic brachia (seen otherwise only in some *Sulcophanaeus*). As indicated by %D in Table 2, *Oxysternon* (particularly *Mioxysternon*, %D = 28) is the more highly evolved of the genera. Tables 2 and 3, however, do not account for synapomorphous states unique to these genera, most notable of which are the spinate metasternum and acute postero-median pronotal angle of *Oxysternon* and the head-prothorax interlocking mechanism of *Phanaeus*.

The relatively low frequencies of synapomorphy (0-1) between this genus group and other taxa indicate phyletic isolation; that is, they support the hypothesis that this genus group can be regarded as a distinct evolutionary lineage. On the other hand, the relatively low incidence of synapomorphic states (3) characterizing the group (i.e., relative overall primitiveness) suggests a relatively slow evolutionary rate (compared to, say, genus group 2).

A rather long phyletic history is indicated by the taxonomic pattern, i.e., the distinctness of taxonomic gaps. Thus, intermediate types minimizing gaps between genera, among subgenera and species-groups of *Oxysternon* and among the species complexes of the *Phanaeus splendidulus* group are virtually non-existent. Conversely, the taxonomic difficulties arising because of the phenetic overlap among constituent subgroups of the *P. vindex* group suggests the hypothesis that this species group, (1) underwent relatively recent (and rapid ?) differentiation and/or (2) its differentiation, whether recent or remote, has been characterized by a comparatively low incidence of extinction. The geographic distribution of the *vindex* group (see below) supports the first alternative, that this species group underwent extensive

radiation in an initially restricted, though highly partitioned geographic theater (Mexico).

Genus-group 2: *Coprophanaeus-Dendropaemon*. Relative to other phanaeines, these genera are highly evolved. Indeed, the extreme phenetic divergence of *Dendropaemon* makes it very difficult to conclude intuitively that there exists a close phyletic relationship between such different taxa as *C. (Megaphanaeus) lancifer* (Figs. 181-182) and *D. (Dendropaemon) nitidicollis* (Figs. 308-309)! However, a close phyletic affinity between these genera is evidenced by a high frequency of synapomorphy (see Table 3): emarginate clypeus and U-shaped clypeal process, *Coprophanaeus*-type labrum, weakly emarginate mentum, and roughened pronotal sculpturing. Moreover, several other tendencies tend to reinforce the relationship (although they are not all considered in Table 3): usual absence of front tarsi in females, similarly developed front tibiae, tendency for secondary sexual dimorphism to be less pronounced than in other phanaeines, specialized feeding habits (assumed of *Dendropaemon*), common occurrence of pronotal ridging, as well as the conservation of a number of primitive aspects of head structure in otherwise quite highly evolved groups (monopodal brachia, persistence of distinct canthal areas, transverse depression of postocular lobes, incomplete occipital ridge, etc.).

On the basis of the high degree of synapomorphy between *Coprophanaeus, sen. str.*, and *Coprophanaeoides*, I have concluded that the latter taxon is an annectant between the two genera. Moreover, it appears that *Coprophanaeus, sen. str.*, is more closely related phyletically to *Coprophanaeoides* than to either *Megaphanaeus* or *Metallophanaeus*. That *Coprophanaeoides* and *Dendropaemon, sen. str.*, are undeniably congeneric is supported by their sharing of a number of uniquely dendropaemine features (see above). Consequently, I must conclude that *Coprophanaeus* is a paraphyletic taxon (*sensu* Henning, 1966) and not a monophyletic one (Fig. 317).

A relative long history of the *Coprophanaeus-Dendropaemon* lineage is indicated by the phenetic isolation of infrageneric taxa as well as the occurrence of "problematic" species. The origin of these taxonomic isolates is more logically interpreted as relict survival of more primitive types; these isolates include *C. (Megaphanaeus) bellicosus, Metallophanaeus* (which is itself likely not monophyletic; see systematic section) and *Paradendropaemon*. The latter is most problematic since, because it lacks many of the salient features of *Dendropaemon*, it cannot be accommodated easily by a strict taxonomic delimitation of *"Dendropaemon."* Indeed, the superficial appearance of *D. ganglbaueri* is more like *Tetramereia* than any of its congeners. Were it not for its possession of unmistakably dendropaemine mouthparts, I would be inclined to rank *Paradendropaemon* as a genus.

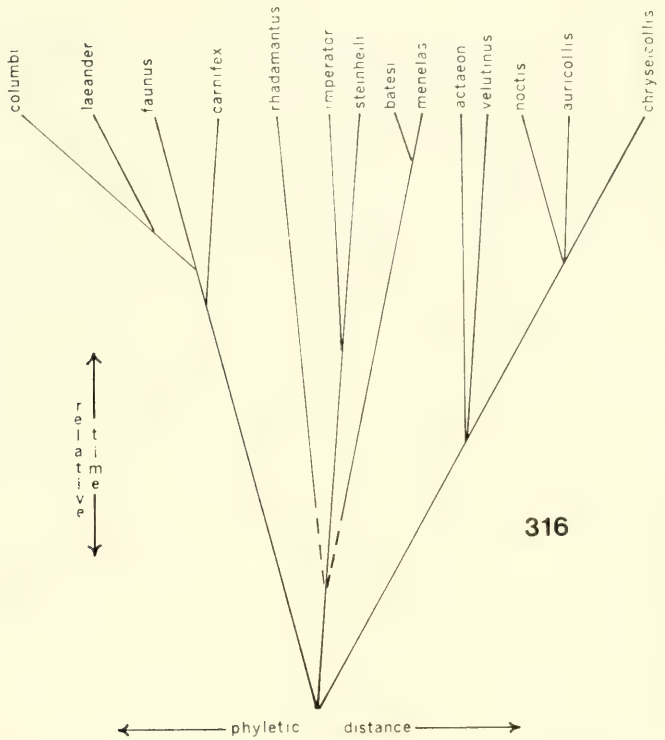


FIG. **316.** Phylogram of the inferred phyletic relationships among species included in *Sulcophanaeus*.

Moreover, the subgeneric rank of *Paradendropaemon* imposes the possibility that *Dendropaemon,* like *Coprophanaeus,* is paraphyletic.

Taxa of uncertain affinities: The phyletic disposition of other phanaeine taxa is not as easily accomplished as that for the aforementioned genus-groups. Relatively speaking, *Diabroctis* and *Sulcophanaeus* are primitive groups most logically interpreted as comprising relict elements. (The disproportionately high %D of 28 of the *S. faunus* group is attributable to the differential possession of derived features [O's in Table 2] by the two constituent species-pairs, and not to apomorphous states shared by all four species; consequently, the %D of any given species in the group is less than 28). There are no derived states shared by all *Sulcophanaeus;* and, as measured by those characters considered in Tables 2 and 3, all species-groups are virtually isolated phenetically and, presumably, phyletically. Moreover, the intragroup variation is such that the phenetic gaps among most constituent species of the species groups of *Sulcophanaeus* are themselves quite distinct. I have concluded, therefore, that *Sulcophanaeus* is very likely a paraphyletic

(or polyphyletic) assemblage which brings together a number of phyletic isolates representing the remnants of numerous older, largely primitive phyletic elements (Fig. 316). This conclusion is supported by the known distribution of the genus (see below). What has been said of *Sulcophanaeus* is also true of *Diabroctis*, which is evidently also a small relict group of phyletic rank equal to that of the species-groups of *Sulcophanaeus*.

A somewhat similar situation exists with *Tetramereia*, *Homalotarsus* and *Megatharsis*, all of which are monobasic. For reasons discussed in the systematic section, the two former genera should probably be merged. As a group, these species appear no more closely related to each other than either is to *Dendropaemon*, which they resemble only slightly more than *Coprophanaeus* (Table 3). In view of their extreme isolation within the phanaeines and of their often curious, unique specializations (e.g., one-segmented labial palpus of *Megatharsis*, unique shape of the tarsomeres of all three species, etc.), I have concluded that they represent highly divergent relicts of doubtful affinities with the *Coprophanaeus-Dendropaemon* lineage. A relictual status of *Megatharsis* and *Tetramereia* is also tentatively suggested by their distributions.

Summary of phylogenetic speculation (Fig. 317): Phyletically, the phanaeine Scarabaeinae, which are presumed to comprise a monophyletic group, appear to consist of two distinct phyletic lineages, together comprising the bulk of known species, as well as a number of phyletically isolated, small groups representing relicts of several older elements. Such phyletic (phenetic) fragmentation is at least compatible with the hypothesis that the phanaeines comprise an ancient group of origin and long-standing residence in South America.

PARALLELISMS

As can be seen in Table 2, for example, given apomorphous character states are not necessarily restricted to presumably monophyletic taxa. In these instances one must ordinarily assume that the derived state arose independently in two or more phyletic lines. The origin of the similarity of two (or more) taxa resulting from joint possession of the same, independently acquired derived state(s) can be interpreted as the result of either parallel evolution or convergent evolution. Differences between these concepts are, to me, more in degree (taxonomic frame of reference) rather than in substance since overemphasis of either kind of similarity will result in the recognition of polyphyletic groups. For present purposes, the presumed independent expressions of a given apomorph *among* phanaeine taxa are here cited as parallelisms while those few cited instances of synapomorphy between phanaeines and non-phanaeines are considered convergences.

Since I am not familiar with a large enough taxonomic variety of

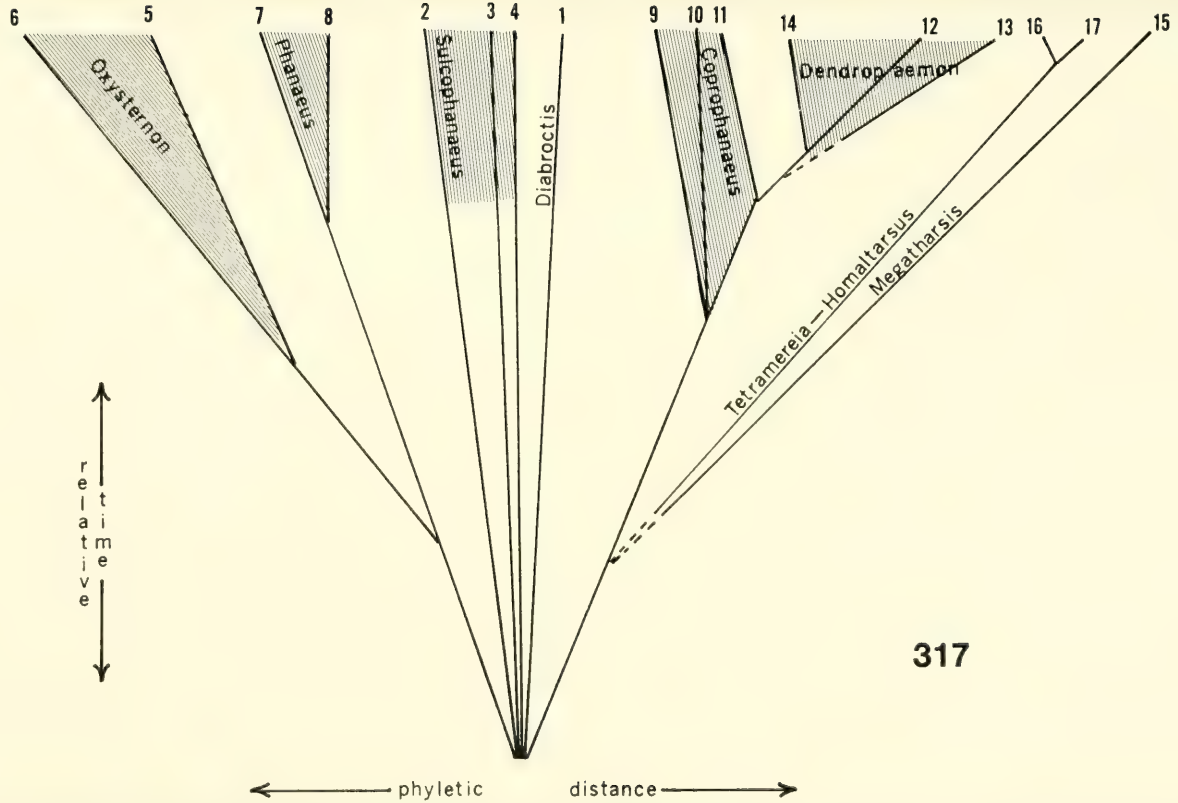


Fig. 317. Phylogram of the inferred phyletic relationships among supraspecific phanaeine taxa. Numbering of branches is the same as in Table 2. Shaded areas link those numbered taxa placed in the indicated genus.

Scarabaeinae to compile a comprehensive list, I have limited a discussion of convergent synapomorphy to mention of the following few instances:

a. transverse clypeal carina: *Diabroctis* and *Onthophagus.*
b. apical hind tibial carina: various phanaeines (see below) and "Coprina" (*Copris* and related genera).
c. lack of tarsal claws: all phanaeines, Eucranini and Onitini.
d. lack of front tarsi in males: all phanaeines, some Onitini, some Canthonia.
e. reduction in tarsomere number: *Dendropaemon, Heteroclitopus* (= *Pinacotarsus*).
f. elongate, flattened body: some *Dendropaemon, Onthocharis, Stiptopodius.*
g. necrophagous habit: *Coprophanaeus* and other species (see below), *Deltochilum,* some *Dichotomius,* some *Canthon.*
h. *Phanaeus*-type antennal club: all phanaeines, *Sceliages.*

Instances of presumed parallelisms among phanaeines are quite numerous. While the following list is not exhaustive, it will serve to illustrate the variety of characters affected and taxa involved. The name of each derived state is followed by those phanaeine taxa within each of which the apomorph is assumed to have arisen.

a. presence of transverse hind tibial carina: *Oxysternon festivum* group; *Diabroctis; Sulcophanaeus carnifex-faunus* pair; *S. imperator-steinheili* pair.
b. large size (length greater than 30mm): *Diabroctis; Megaphanaeus; Sulcophanaeus faunus* group.
c. reduction of tarsomere number: *Dendropaemon; Tetramereia;* (? *Paradendropaemon*).
d. bipodal cephalic brachium: *Phanaeus-Oxysternon* genus-group; *Sulcophanaeus imperator; S. laeander-columbi* pair.
e. corniform female cephalic process: *Megaphanaeus; Sulcophanaeus faunus* group.
f. intrasternal position of last abdominal spiracle: *Megaphanaeus; Sulcophanaeus faunus-carnifex* pair; *Mioxysternon.*
g. loss of front tarsi in female: *Metallophanaeus; Coprophanaeus, sen. str.; Tetramereia-Homalotarsus; Sulcophanaeus carnifex; S. steinheili.*
h. flat elytral interstriae: *Sulcophanaeus auricollis* group; *Megaphanaeus; Phanaeus damocles-quadridens; P. vindex-difformis.*
i. rugose elytral interstriae: *Megaphanaeus; Phanaeus vindex* complex.
j. carinulate striae: *Megaphanaeus; Dendropaemon; Phanaeus bispinus; P. kirbyi-palaeno* pair.
k. notching of hind wing: *Coprophanaeus, sen. str.-Dendropaemon; Phanaeus bispinus.*

l. roughened pronotum: *Coprophanaeus-Dendropaemon* genus group; *Phanaeus vindex* group; *Sulcophanaeus laeander-columbi* pair; *Tetramereia-Homalotarsus (-Megatharsis).*

m. spiniform clypeal process: *Oxysternon festivum* group; *Phanaeus kirbyi-palaeno* pair.

n. necrophagous habit: *Coprophanaeus;* isolated species of *Phanaeus* (e.g., *bispinus, meleagris*); isolated species of Sulcophanaeus (e.g., *faunus*).

Evolutionary Implications of Phanaeine Ecology and Distribution

Halffter and Matthews (1966) discuss quite fully various aspects of the ecology and behavior of Scarabaeinae. Rather than redevelop their discussion as it applies to phanaeines, comment here will be limited to the following summary statements:

1. The principal food sources of phanaeines are animal feces (particularly the dung of large herbivores such as cattle) and carrion.

2. Necrophagy as such is likely a behavioral adaptation for forest existence and a derived behavioral pattern in Scarabaeinae (see Halffter and Matthews for a detailed argument). Dung beetles in South American forests are very often necrophagous; conversely, few necrophagous species inhabit grasslands. This behavorial pattern usually cuts across established taxonomic lines, such that very few taxa can be delimited by necrophagous feeding behavior as well as by morphology. *Coprophanaeus* is one of these few. Ecological experiments designed to test the relationship between necrophagy and forest habitat have not been done. Among other things, these might investigate (a) the apparent scarcity of carrion in open grassland compared to a forest, (b) rates of desiccation of carrion in a forest vs. grassland, and (c) the frequency and severity of competition between necrophagous animals in a forest vs. in a grassland (e.g., between beetles and vultures in grasslands).

3. Within the phanaeines the taxonomic distribution of principally diurnal-coprophagous-grassland species and nocturnal-necrophagous-forest species is largely generic. Thus, most *Phanaeus* are coprophagous-grassland forms while *Coprophanaeus* consists entirely (as now known) of necrophagous-tropical forest species. These two genera include about 60% of all phanaeines. *Diabroctis, Sulcophanaeus* and *Oxysternon* are poorly known ecologically, but all appear to be largely coprophagous groups with both grassland and forest species. Nothing is known about the biologies of *Dendropaemon, Tetramereia, Homalotarsus* and *Megatharsis.*

Phanaeines are restricted to the New World, occupying South America (except Chile and southern Argentina), Central America, Mexico and eastern and extreme southwestern portions of the United States (Maps 1-6). The

TABLE 4. Summary of the distribution and relative abundance of phanaeines.*

Taxon	Region				
	1	2	3	4	5
Diabroctis	(+)	—	—	—	—
Sulcophanaeus	(++++)	(+)	+(+)	+	—
Oxysternon	(+++++)	—	—	—	—
Phanaeus					
splendidulus complex	(++)	(++)	(1 sp)	(2 sps)	—
vindex complex	—	—	(+)+	(++++)++	+(+)
Coprophanaeus					
Megaphanaeus	(+)	—	—	—	—
Metallophanaeus	(+)	—	—	—	—
Coprophanaeus, s.s.	(+++++)+	1 sp	+	+	—
Dendropaemon	(+++++)	—	—	—	—
Megatharsis	(1 sp)	—	—	—	—
Tetramereia	(1 sp)	—	—	—	—
Homalotarsus	(1 sp)	—	—	—	—

* See text for explanation.

only insular species is *Sulcophanaeus carnifex*, which is endemic to Jamaica. Table 4 summarizes the distribution according to the following numbered regions:

1. Tropical South America (except northwestern sector and areas west of the Andes)
2. Temperate South America
3. Northwestern South America (including areas to the Pacific side of the Andes) and Panama
4. Central America (except Panama) and tropical Mexico
5. Temperate Mexico and the United States.

In Table 4 presence in one or more regions is denoted by one or more +'s, or by the number of species if very few; — denotes absent. The number of +'s indicates relative abundance in a given region; parentheses enclose that portion endemic to the region.

The tropical South American fauna includes representatives of all phanaeine genera, eight of which are endemic or largely so. Such a high degree of generic endemism strongly suggests South America as the place of origin of the group. Differentiation of all genera (as presumably could also be the case for other South American scarabaeine groups) was probably before or during Tertiary isolation of South America. If during Tertiary isolation, the greatest development of phanaeines could have coincided with that of South American herbivores (e.g., the ungulates). During periods of

isolation inter-American water gaps presumably made difficult northward dispersal of both dung beetles and large land animals with which they were associated. If the initial development of scarabaeine groups in all geographic areas were closely tied to the presence of a large food supply provided primarily by the dung of large animals, the extinction from South America of grassland herbivores must have greatly affected the evolution of the scarabaeine fauna. Necrophagous, forest dwelling groups, such as *Coprophanaeus,* could have resulted from movement of grassland groups into forest habitats in response to extinction of herbivores. The coprophagous groups which survived were probably largely restricted to small, geographically isolated refugia where they differentiated as small, phenetically quite dissimilar groups.

The disjunct patterns of distribution within the *faunus* and *imperator* groups of *Sulcophanaeus* are indicative of relict groups and, hence, compatible with the hypothesis presented above that the genus comprises the relicts of several older phyletic elements. The following disjunct patterns between closely related species are not evident in Map 1:

a. *Sulcophanaeus faunus,* Amazon Basin—*S. carnifex,* Jamaica.
b. *S. laeander,* Venezuela (savannas?)—*S. columbi,* southern Amazon Basin.
c. *S. imperator,* Andean highlands of northern Argentina and of Bolivia—*S. steinheili,* high mountain valleys of Colombia.

The distribution of the *auricollis* group (Map 1) is evidently continuous. This appears to be the only sulcophanaeine group that has undergone even limited northward dispersal and differentiation. The close resemblance of the Andean species *auricollis* and the Mexican *chryseicollis* and the occurrence of two species (*noctis* and *velutinus*) in both South and Central America suggest that the movement was relatively recent, perhaps accompanying the equally limited northward dispersal of *Coprophanaeus, sen. str.* (Map 5) and the *Phanaeus splendidulus* group (Map 2) (see below).

While the relict status of *Megatharsis* and *Tetramereia* (and *Homalotarsus*) is supported by the extreme phenetic and geographic isolation of these species (Map 6), both are very poorly represented in collections and may later prove to be more widely distributed (in the case of *Megatharsis*) or more evenly distributed (*Tetramereia*). Likewise, the distribution of *Dendropaemon* is poorly known and, therefore, not amenable to serious geographic analysis.

Within other genera distributional patterns appear more regular, i.e., with closely related species occupying largely adjacent regions. There is a tendency, however, for phenetic isolation to be coincident with geographic isolation (e.g., in the cases of *Coprophanaeus pertyi* and *pessoai, C. bellicosus,* and the species of *Mioxysternon*). The northward dispersal and

accompanying linear differentiation (speciation) of the *S. auricollis* group is paralleled in *Coprophanaeus, sen. str.*, by the *dardanus* group (*C. telamon* extending from South America into Central America and southern Mexico; *C. pluto* endemic to Mexico) and in the *Phanaeus splendidulus* group by the *endymion* complex (*P. blanchardi* in northwest South America, *pyrois* in Central America and *endymion* in Central America and southern Mexico).

The *Phanaeus vindex* group is the only phanaeine taxon centered geographically outside South America. This large species-group is centered in Central America and adjacent southern Mexico, where it almost certainly originated and underwent extensive, probably rapid radiation (as indicated by the narrow, taxonomically inconclusive phenetic gaps between clusters of closely related species). From Mexico the group dispersed both northward and southward, differentiating further in both directions, although most clusters remained in or near the locus of radiation. Northward movement of Mexican species undoubtedly gave rise to a temperate fauna (the *vindex* complex) largely endemic to the United States. Although the possibility needs to be examined more closely, the distributions of U.S. species indicate that their history includes disruptions by Pleistocene glaciation (suggested by my somewhat premature suspicion that *P. floridanus* and isolated populations of *P. vindex* in Arizona are products of differentiation in refugia from glaciation). The *hermes* cluster, conversely, likely arose from South American immigrants moving southward from Mexico. Apparently the only group to disperse successfully in both directions was the *mexicanus* cluster. The combined range of the constituent species of this cluster extends from Peru *(lunaris)* through Central America *(wagneri)*, southern Mexico *(mexicanus)*, and along the western coast of Mexico into Arizona *(amythaon)*. The ecological-geographical distribution of *Phanaeus* in Mexico is quite complex and in need of continued analysis.

In trying to assess the significance of geographical patterns of phanaeine distribution, two points come to mind. First, field work in areas like the Amazon Basin is restricted logistically to efficient avenues of penetration, i.e., mostly large rivers. Thus, one can gather data yielding sound ideas about beetles collected along and near rivers but no ideas about what occurs in areas between rivers, which in the Amazon Basin are immense pieces of real estate. Consequently, inferences about distributions of largely Amazonian groups are subject to the hypothesis that, because the area appears monotonously "homogenous" from an airplane, the unworkable inter-river areas may be assumed to be faunistically similar to areas along and near encompassing rivers. This is a logical, and probably largely accurate expectation. But just how "homogenous" are the 2.5 billion or so acres called the Amazon Basin? Second, an important consideration is the possible effects of human activity on the recent movements and abundance of dung

beetles. The livestock industry in all parts of the world has undoubtedly resulted in the geographic expansion and increased abundance of a great many coprophagous forms. Seemingly, the faunas least affected by such activity would have been those supported prior to the introduction of livestock by indigenous herbivores, such as the bison in the North American Great Plains and the rich herbivore fauna of African savannas. The positive effects of the introduction of livestock has no doubt been great in Latin America, which in recent, pre-European times supported a very depauperate indigenous herbivore fauna. Many coprophagous species of phanaeines and other dung beetles now considered very common were perhaps quite scarce in those times. A small scale example is the case of *Sulcophanaeus carnifex,* which today can be collected in incredible numbers in cow dung on Jamaica (Matthews, 1966); Jamaica has presumably never supported large herbivores other than cattle, the only known mammalian fossils being bats, monkeys and small rodents. On the other hand, the same livestock producing activities, which always involve the cutting of forests for pasturage (or timber, crops, etc.), has undoubtedly had some negative affect on the distribution and abundance of stenotopic forest species, whose habitat is shrinking at a tremendous rate in many parts of Latin America.

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APPENDIX: MATERIAL STUDIED

Following is a list of species examined for this study arranged according to the classification proposed above. After each species name is noted parenthetically the degree to which each was studied by the following letter code:

c—completely; all skeletal features studied in detail.

m—examined externally but mouthparts extracted; internal features not observed.

e—examined externally only; mouthparts not extracted.

If only one or two specimens were studied, their sex and number are also given. In addition, a list of the non-phanaeine beetles follows that of phanaeines; all these species were examined completely.

Diabroctis

mimas (c); *mirabilis* (m); *cadmus* (m, 1 male).

Sulcophanaeus

faunus (c); *columbi* (m); *laeander* (m); *carnifex* (c); *imperator* (c); *steinheili* (m, 1 male, compared with type by Pereira); *rhadamantus* (c, 1 pair); *batesi* (c); *menelas* (c); *auricollis* (e); *chryseicollis* (c); *noctis* (m); *velutinus* (m); *actaeon* (m).

Oxysternon

festivum (c); *macleayi* (e); *lautum* (c); *conspicillatum* (c); *ebeninum* (e); *palaemon* (c); *sericeum* (m); *smaragdinum* (m); *silenum* (m); *curvispinum* (m); *pteroderum* (e, 1 male).

Phanaeus

splendidulus (c); *melibaeus* (m); *dejeani* (m); *palaeno* (c); *kirbyi* (m); *haroldi* (c); *bispinus* (c); *chalcomelas* (c); *meleagris* (m); *endymion* (c); *pyrois* (m); *blanchardi* (e, 1 pair); *lunaris* (m); *achilles* (m, 1 male); *lugens* (m); *prasinus* (m); *hermes* (m); *mexicanus* (c); *amythaon* (m); *wagneri* (m); *demon* (c); *obliquans* (m); *quadridens* (c); *damocles* (m); *palliatus* (m); *eximius* (m, 1 pair); *adonis* (c); *pilatei* (m); *sallei* (m); *beltianus* (m); *guatemalensis* (m); *amethystinus* (m); *scutifer* (e, 1 male); *melampus* (m); *daphnis* (c); *tricornis* (m); *tridens* (m); *nimrod* (m); *furcosus* (m); *vindex* (c); *difformis* (c); *triangularis* (c); *floridanus* (c).

Coprophanaeus

jasius (c); *cerberus* (c); *parvulus* (c); *spitzi* (c); *milon* (c); *telamon* (c); *dardanus* (c); *pluto* (m); *saphirinus* (c); *horus* (m, 1 pair); *pertyi* (m); *pessoai* (e); *lancifer* (c); *ensifer* (c); *bonariensis* (c); *bellicosus* (c).

Dendropaemon

denticollis (c); *haroldi* (m); *fasces* (e); *nitidicollis* (m); *smaragdinum* (e); *viridipennis* (m); *amyntas* (m); *fractipes* (m); *lobatum?* (m); *piceum* (m); *viridis* (c); *telaphum* (m); *renatii* (m); *hirticollis* (m); *bahianus?* (m); *ganglbaueri* (m, 1 female).

Tetramereia convexa (c).

Homalotarsus impressus (e, 1 female).

Megatharsis buckleyi (m, 2 females).

Non-Phanaeines examined (all are Scarabaeinae unless indicated otherwise)

Anomiopsoides sp.; *Heliocopris* sp., *Canthon pilularis* (L.); *Dichotomius* sp.; *Onitis* sp.; *Eurysternus sulcifer* Balths.; *Deltochilum brasiliense* (Cast.); *Scarabaeus* sp.; *Catharsius molossus* (L.); *Copris* sp.; *Phyllophaga* sp. (Melolonthinae); *Pseudolucanus* sp. (Lucanidae).

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A Revision of the Subfamily Chlamisinae of America North of Mexico (Coleoptera: Chrysomelidae)[1]

Jay B. Karren

ABSTRACT

In this revision 29 species are figured and described with three Mexican species figured and described to a limited extent. Keys to the species and genera of this area are included. Although primarily taxonomic, this work brings together available data concerning variation, distribution, host plants, parasites and predators. Five new species, *Pseudochlamys semirufescens, Chlamisus flavidus, C. nigromaculatus, Neochlamisus velutinus,* and *N. bimaculatus* are described.

A study of the genitalia has made possible a better understanding of the group and has indicated more reliably the evolutionary relationships among species and genera, so that meaningful statements about zoogeography and possible dispersal patterns in the group can be made. On the basis of genitalic characters, a new genus is proposed for some species formerly included in the genera *Chlamisus* and *Diplacaspis*. *Pseudochlamys* is recorded in North America for the first time by the description of one new species.

A study of the food plants revealed that most have a wider range and host distribution than was initially supposed. Although a particular species may be limited to one host in a small geographical area, in other localities the host preference can be quite different. Some food plants are acceptable to several species. Field observations and museum labels show that some North American chlamisines feed on a wide variety of host plants, while others are host specific.

INTRODUCTION

This is a revision of the species of Chlamisinae occurring in America north of Mexico, together with records of biological observations on these species. It is based on a study of 4,878 specimens, field studies of two species, and a preliminary study of many Mexican and Central American species.

Most insect collectors easily overlook the Chlamisinae because both adults and larvae of many kinds of these small beetles superficially resemble caterpillar droppings or other bits of debris. As a result, chlamisines are not common in collections and have not attracted the level of taxonomic attention given the other chrysomelid subfamilies. Although some of the North American species were among the first known in the subfamily, the few revisionary studies of Chlamisinae have not treated them in much detail but have dealt primarily with the more numerous and more strikingly colored Neotropical chlamisines. This revision was undertaken in the hope of clarifying the taxonomic status of the various recognizable forms occurring in America north of Mexico, making known something of the biology of the group, and describing the supposedly phylogenetic relation-

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ships among species and species groups, both in the region treated and between these groups and their Mexican and more southern relatives.

Of the 32 names that have been proposed in this group, seven are placed in synonymy, two are misidentifications of Mexican species, and two are names that cannot be associated with any species because of lost type material and inadequate descriptions. The last two could be junior or senior synonyms of recognized species; but for inability to identify species involved and in the interest of nomenclatural stability, neotypes will not be designated. Five species are described as new. Descriptions and figures of 26 North American species are included and three Mexican species are figured and described to a limited extent. These latter are included because the information about them will aid in identifying other North American species and will contribute to an understanding of the species groups involved.

The inadequacy of Lacordaire's (1848) classification of Chlamisinae has been recognized for a long time, although no one has attempted to revise the entire group. A preliminary study indicated that genitalic characters are useful in determining the species and their relationships. A study of the genitalia has made possible a better understanding of the group and has indicated more reliably the evolutionary relationships among species and genera, so that meaningful statements about zoogeography and possible dispersal patterns in the group could be made. On the basis of genitalic characters, a new genus is proposed for some species formerly included in the genera *Chlamisus* and *Diplacaspis*. *Pseudochlamys* is recorded in North America for the first time by the description of one new species in that genus. *Chlamisus* is probably still heterogeneous, but further study is needed of the Mexican and Central American species before any further generic distinctions can be drawn.

My previous study of the genus *Exema* (Karren, 1966) indicated certain monophagous tendencies within the subfamily. Brown's study of the Canadian Chlamisinae (1943) indicated that each species is restricted to one particular host. Further study of the species described by Brown revealed that most have a wider range and host distribution than was initially supposed. Some food plants are acceptable to several related species. Although a particular species may be limited to one host in a small geographical area, in other localities the host preference can be quite different. Field observations and museum labels show that some North American chlamisines feed on a wide variety of host plants, while others are host specific. There is a need for more accurate and extensive field observations of host preferences.

The life histories of a very few species have so far been made known. Through laboratory rearings and field observations, additional information has been obtained on several species. Data on habits and life history

stages increase the understanding of the relationships among the species. Laboratory rearing of specimens has also revealed considerable parasitism of eggs, larvae and pupae by Ichneumonidae, Chalcididae and other Chalcidoidea.

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MATERIALS AND METHODS

Specimens for this study were borrowed from all of the major collections in North America and several European museums, as listed in the Acknowledgments. Type specimens have been examined whenever possible and compared with other material used in this study. It has not seemed necessary at this time to designate neotypes for those types that are lost. Some collections and field observations were made to supplement the data obtained from museum specimens.

Unfortunately, biological data, even names of host plants, are entirely lacking for a few of the rare species. Only more careful field studies in the future will provide such information.

Label data on specimens were recorded in a uniform manner, in some cases requiring interpretation where numbers represent dates or standard abbreviations are not used. Complete label data are recorded for type material. For the distribution of species in the United States and Canada, only the county is given (for type specimens, placed in parentheses if not originally included on the locality label). There is a distribution map for each species on which the spots usually represent counties in the United States, except more specific localities are indicated in the large western counties and political divisions of countries other than the United States. More definite information is recorded, when available, for localities outside the United States and Canada. Major political divisions of Canada, Mexico and the Central American countries are cited in the same way as states. Localities that are not definitely identified are placed in quotation marks. Inclusive collecting dates are designated whenever two or more labels indicate a collecting span of ten days or fewer.

For detailed study, especially of poorly mounted material on cards and points, the specimens were first treated with relaxing fluid (95% ethanol, 106 cc; distilled water, 98 cc; benzol, 14 cc; ethyl acetate, 38 cc) for about 15 minutes or until the legs were pliable. The legs and antennae were then spread into more extended positions for study, the specimen mounted on an insect point and allowed to dry. Broken parts were mounted on the upper surface of the point. The male genitalia or female spermathecae were removed and placed in hot KOH for about 10 minutes, then transferred to 70% alcohol to which a drop or two of acetic acid had been added. Removal of the ejaculatory guide from the aedeagus was usually done in 70% alcohol in a Syracuse dish. Minuten pins and small cover slips were helpful in orienting the parts in a proper position for study and drawing. Genitalia were later placed in small vials which were attached to the pin of the mounted specimen.

All drawings and measurements were made with the aid of an ocular grid in a steroscopic microscope, using 15×, 60×, and 120× magnifications.

Terminology is taken from "A Glossary of Entomology" by Torre-Bueno (1937). More detailed information on special terms and their use in the species descriptions will be found in the discussion of the general and taxonomic characters of the subfamily. Terms used for the male genitalia are those used by Powell (1941). The female spermathecae are described using the terms of Spett and Lewitt (1926).

The following abbreviations are found in parentheses with the listings of types and paratypes indicating the private collection, museum or university in which the types are to be found.

AMNH	American Museum of Natural History
CAS	California Academy of Sciences
CDA	Canada Department of Agriculture
CU	Cornell University
ENA	Escuela Nacional de Agricultura, Chapingo, Mexico

HFH	H. F. Howden collection
INHS	Illinois Natural History Survey
ISU	Iowa State University
JAW	J. A. Wilcox collection
JBK	J. B. Karren collection
MCZ	Museum of Comparative Zoology, Harvard University
MZU	Museum Zoologicum Universitatis, Helsinki
OSU	Ohio State University
SDSU	South Dakota State University
TAMU	Texas A & M University
UAR	University of Arizona
UK	University of Kansas
UM	University of Missouri
USNM	United States National Museum

Illustrations

Structures of special taxonomic value are illustrated. Where there is variation in an illustrated structure, this is described in the treatment of the species but the drawing is of the most common form.

Illustrations for each species usually include the entire beetle (dorsal, lateral and cephalic aspects), prosternum, aedeagus (dorsal and lateral aspects), ejaculatory guide (dorsal and lateral aspects) and the spermatheca. A few drawings have been made of antennae and tarsal claws when deemed necessary to differentiate two or more forms. Comparable illustrations have been made to the same scale for all species.

In the drawings of the dorsal and cephalic views of the beetles, the right side is used to indicate color patterns and the left side punctation and sculpturing.

Each pair of drawings of the entire beetle, aedeagus, and ejaculatory guide is numbered as one illustration and represents first the dorsal then the lateral aspect of each structure. The dorsal aspect of the aedeagus is drawn with the large apical portion as nearly horizontal as possible, reducing the visible amount of the curved section over the basal foramen. An accurate representation of the size of this section is found in the lateral aspect. In a few cases the ventral aspect of the ejaculatory guide is shown to illustrate details not shown in the other two aspects.

GENERAL AND TAXONOMIC CHARACTERS

A formal description or diagnosis of the subfamily will not be given; instead, a discussion of the characteristics which have been used in the descriptions and those which otherwise warrant some explanation will be given. Any structure that is of the same generalized shape throughout the subfamily will be referred to as normal here and omitted in the descriptions.

North American species of the subfamily Chlamisinae are small insects ranging from 2.1 to 6.0 mm long. The species of *Exema* and *Pseudochlamys* are among the smallest forms in North America. The genera *Neochlamisus* and *Chlamisus* exhibit a wide range of variation, with species among the smallest and the largest in North America.

Color in North American chlamisines varies from yellow to metallic black. The beetles may be either uniformly colored or with various color patterns that are distinctive for the species. The colors of most North American species are metallic to some extent. This condition is obvious without the aid of a microscope in most species, but in others only small areas under high magnification reveal their metallic nature.

The head is usually the same color as the rest of the insect, but it may be differently colored, in which instances the color pattern is a secondary sexual characteristic. The antennae are entirely yellow or light brown, or the distal segments may be dark brown. The color change can be abrupt or gradual toward the apical segments. The labrum is yellow to light brown, the other mouth parts darker. The undersurface is generally similar to the rest of the body in color except that it is variously marked with black in the yellowish forms from the Southwest. The legs are generally uniformly colored like the rest of the body, although in a few species they are yellow to light brown or yellow banded.

As seen from above, the general body shape in the group is subquadrate, a little narrowed behind. Many species are distinctly more elongate than others. The cuticle has a characteristic finely granulated appearance, more obvious in some species and on some structures than in others. Such granulation is here described as strongly granulate as opposed to vermiculate, punctate or striate. Any structure lacking punctures, tubercles or carinae is described as smooth although it still may have the familiar granulate appearance.

Faint, shallow or deep depressions called foveae are common in most species on various body structures but are most common and usually deepest on the metasternum. Often the closely set foveae and punctures produce a reticulate condition. The foveae are usually more strongly granulate than the surrounding area, and the center of each is occupied by a faint to deep puncture. The foveae on a structure may be so confluent that only small, irregular carinae remain. The elongate tubercles and connecting ridges between two or more tubercles on the elytra are also called carinae.

Many different sizes and shapes of parallel impressed lines and ridges are found on many parts of chlamisines. The former are called striae, although they are not the usual longitudinal lines on the elytra referred to by coleopterists. They are found on the pronotum, on the elytral tubercles and carinae, inside large punctures and foveae and on almost any other part of the body. Some striae become so convoluted and irregular that the surface is called vermiculate. Ridges are referred to as carinae.

There is a great deal of variation in the punctures of the cuticle. They can be so small or faintly impressed that they can only be perceived with difficulty under high magnification. Others are small but very deep and

some are deep with a large impressed surrounding area. Most punctures have a single seta in the center, ranging from so small that it is difficult to see to large, long and obvious. In at least one species (*Chlamisus maculipes*) there are several hairs in each puncture. Three punctate conditions are commonly described: finely punctate, when the punctures are more widely separated than their diameters; moderately punctate, when the distance between punctures and their diameters are approximately equal; and coarsely punctate, when punctures are separated by less than their diameters. In addition, deep punctures are those deeper than their diameters; shallow punctures are shallower than their diameters. Faint punctures are barely visible under high magnification. The foveolate, striate and punctate conditions described above in several states are actually a continuum. The terms are used only for convenience of description and their usefulness depends heavily on the observer's judgment.

The head is inserted inside the anterior section of the pronotum. It appears circular when viewed from the front. The large lateral eyes are deeply emarginate just above the antennal sockets. In the dark or metallic species the area of the frons in the emargination of the eye usually has a large yellow spot. Three areas of the frons are commonly referred to in the descriptions. The lower frons is that portion below the level of the antennal sockets. Above this and between the emargination of the eyes is the middle frons. The area above the middle frons and below the vertex is the upper frons.

The mouthparts are received between the clypeus and the large prosternum. The antennal grooves are located lateral to the prosternum, between it and the procoxae. In some species there is an antennal fovea on the lower frons just ventral and medial to each antennal socket. The undifferentiated clypeus and lower frons between and below these foveae are often depressed and punctate. The middorsal area of the upper frons below the vertex is also often depressed or longitudinally grooved.

The antennae have been used for a long time as one of the basic characters for the classification of chlamisines. Less significance is placed on them in the present paper because of interspecific variation in the antennal segments and their noncorrelation with other characters. There are, however, some general patterns of antennal characters that are of use in establishing relationships.

The scape is similar in most of the chlamisines. It is the longest antennal segment, slightly curved and enlarged apically. The small subglobular pedicel is attached to its apex. The remaining segments are gradually flattened toward the apex. The width of these flattened segments refers to their greatest width. The third antennal (first flagellar) segment is usually subcylindrical and a little longer than the preceding. In some

cases it has a slight apical enlargement on the ventral side. The next 1-3 segments can be similar to each other and subequal, or each may be subconical with a slightly broader and deeper enlargement than that of the preceding segment. The apical 4-5 segments are rectangular in outline and usually a little broader than long. The apical segment is always subconical, a little larger than the preceding segments and rounder at the apex. In previous treatments of the chlamisines the antenna is described as serrate, but it is not clearly understood by coleopterists which segment is to be considered the beginning of the serrate portion of the antenna. I have avoided this problem by calling segments subtriangular when they are apically as wide as long, but narrowly constricted at the base. Segments that are wider than long but still not rectangular are called subrectangular. The basal flagellar segments which are longer than their apical widths are called subcylindrical.

The pronotum is faintly to highly gibbose, usually with a longitudinal groove that partially divides the gibbosities. The pronotum can be either punctate, striate or both, depending upon the species or species group. The pronotum is either nontuberculate or possesses tubercles according to a definite pattern.

The tubercles on the pronotum and elytra follow the same general pattern as discussed by Karren (1966), except that they are usually more highly developed and in some cases more numerous than the entire complement suggested. Tubercles sometimes are shifted slightly in position, but never so much that they cannot be recognized. The terminology used in the above mentioned paper with a few additions is adequate for purposes of this study. The term marginal carina refers to a variable ridge extending from the umbone to just before the apex of the elytron near the lateral margin. Carinate tubercles are found in the positions of named tubercles, but extend more or less to other tubercles.

The mesoscutellum is always visible as a subquadrate structure behind and between the posterior lobes of the pronotum. The sides converge more or less anteriorly, depending upon the group. The anterior margin, which consists of three rounded processes, is usually covered by the pronotum. The central process may develop between the posterior processes of the pronotum and extend as a rounded carina along the center of the scutellum for various distances. The posterior margin may be straight, depressed, broadly emarginate or both depressed and emarginate. The posterolateral angles are reflexed when they project above the elytra. The metascutellum or second scutellum may or may not be exposed just behind the mesoscutellum and between the elytra. In those species where it is visible, it is usually sharply carinate.

Behind the mesoscutellum the elytral suture is usually straight for a

short distance. The remainder is strongly serrate to the apex. The proportion of the suture that is straight varies among the species, except that it is completely serrate in all species of *Exema* and in *C. quadrilobatus*. Several Neotropical species have an entirely straight suture.

The pygidium is always completely exposed beyond the ends of the elytra. It is carinate, tuberculate, vermiculate or foveolate with various degrees of punctation. The apex is narrowed, rounded, not truncate, and extends slightly anteriorly beneath the abdomen. Two large lateral depressions are usually evident on the apical one-third of this structure. Four similar depressions are also found near the base.

The most common form of the prosternum is coarsely punctate and goblet-shaped. The anterior half is broad and the sides are gradually or suddenly convergent to a long prosternal process, which fits tightly between two anteriorly projecting processes of the mesosternum. There is actually a third central process on the mesosternum, which fits into the hollow, dorsal, apical portion of the prosternal process. Variations in the prosternum include almost straight and convergent lateral margins resulting in a subtriangular shape. In other species the prosternal process is enlarged, flattened, evenly rounded or longitudinally grooved toward the apex. The large anterior half of the prosternum is either flat or with a large central depression. Just behind the anterior margin, which flanges beneath the mouthparts, there may be a transverse groove.

The broadly exposed sclerites of the sternum are the large medial metasternum, divided by a complete longitudinal groove, and the smaller lateral metepisternal plates. These are usually deeply foveolate or roughly sculptured. The five visible segments of the abdomen, especially the first and the last, are similarly sculptured. The intervening segments 2-4 are shortened so that only the posterior margins are exposed and sculptured. Any reference to the abdomen in a description refers to one or more of these ventral segments.

The anterior and middle pairs of legs in repose are received in broad grooves on the ventral surface, bordered by the lateral pronotal margin, the prosternum, and the anterior margin of the metasternum. The posterior pair of legs is received in depressions formed in the first visible abdominal segment just posterior to the metasternum. Each femur has a small longitudinal groove to receive the tibia. An acute, usually inwardly curved, apical process on the posterior angle of each front tibia is usually found in males that I have studied, though in a few species it is paired. A similar process is found on the middle tibia of some males and the front and middle tibiae of some females. These are called tibial spines in the descriptions and keys.

The tarsal segments are of the generalized chrysomelid type. The first

two segments are subtriangular, the third is strongly bilobed, the fourth is hidden between the lobes of the third segment, and the fifth is long and slender. The tarsal claws are simple, broadly toothed or bifid; the form usually has generic or specific significance.

MORPHOLOGY AND TAXONOMIC USE OF GENITALIA

The male genitalia provide many characters of taxonomic and evolutionary significance. Previous study of chrysomelid genitalia and their importance has been of a general nature. Powell (1941) studied the male genitalia of most of the subfamilies but included only a few representatives of each group and only one chlamisine species. Spett and Lewitt (1926) did a similar study of the female spermatheca that included one species of *Chlamisus*. Several other less extensive studies of minor importance have also been undertaken. The most important contribution to an understanding of the male genitalia was included in a revision of the Chlamisinae of Argentina by Monrós (1952). This included a number of line drawings of the entire or apical half of the male aedeagus. Very little has been said about the structure and sclerotization of the internal sac of the aedeagus, but important indications of the relationships of species can be obtained from a comparative study of these sclerotized parts, as will be shown below. Taxonomic use has been made of such information for the first time in this study.

The largest structure among the male copulatory organs is the long, tubular aedeagus. Closely associated with the aedeagus are the tegmen, the spiculum gastrale, two elongate lateral plates and the first post-pygidial tergite. This tergite and the lateral plates are similar in all the species studied and therefore will not be considered further. The Y-shaped spiculum gastrale is also of generalized form in the material studied and indicates a certain degree of affinity of Chlamisinae to the closely related subfamilies. More variable but still rather uniform within the subfamily is the Y-shaped tegmen, the lateral forks of which partially embrace the aedeagus just posterior to the basal foramen. A basal strut of the tegmen extends forward below the aedeagus and partially covers the large foramen. A continuous membrane attaches along the entire lateral edge of the tegmen, extends dorsally around the posterior aedeagus, and forms a membranous sleeve through which the aedeagus passes.

Important specific and generic characters are found in the size and shape of the aedeagus. The most generalized form, found in many chlamisines, many closely related subfamilies, and to a lesser extent throughout the chrysomelids, is the short, tubular aedeagus with an apical orifice and basal foramen. Various modifications in the shape of the apex and the form and placement of apical hairs furnish characters for specific identification. More

specialized chlamisines have the "apical" orifice (Powell, 1941) more centrally situated on the aedeagus. The apical portion of the aedeagus is also variously modified, usually flattened dorsoventrally with a ventrally curved apex. The dorsal wall of the anterior half of the aedeagus is curved ventrally and less sclerotized than the posterior portion. The basal foramen is found on the ventral side of this anterior portion.

An internal sac lies anteriorly within the aedeagus and is continuous with its apical orifice. The walls of this sac are either membranous or sclerotized to varying degrees, offering further diagnostic characters. A sclerotized plate in the dorsal wall of the sac is continuous with the median dorsal plate attached to the anterior edge of the apical orifice. Internally this plate forms a projecting hook of various shapes that is exserted during copulation. Attached to the anterior end of the sac is the ejaculatory guide, a sclerotized structure with numerous modifications of taxonomic use. The generalized tubular shape of the guide is found in *Pseudochlamys, Exema,* and some species of *Chlamisus.* In *Neochlamisus* the structure is more specialized, consisting of two closely fitting asymmetrical plates with a ventral sheath that varies in size and shape. The ejaculatory duct enters the sac through a basal orifice near the anterior end. In those forms with a sheath, the basal orifice is just behind the base of the sheath and between the asymmetrical plates near their proximal end. The posterior edge of this orifice can be seen in cleared material. Its position in relation to the total length of the ejaculatory guide is of taxonomic value. Muscles for retracting the sac attach to its anterior end and lie in the anterior aedeagus. The long ejaculatory duct passes through this end of the aedeagus and through the large basal foramen.

The female genitalia are more uniform throughout the subfamily than the male structures, and the slight differences are hard to evaluate except for those of the spermatheca. This structure has several characters that can be used taxonomically and in phylogenetic studies. The highly sclerotized spermatheca is attached to the common oviduct by a sclerotized spermathecal duct, which varies from long and highly convoluted to short and straight. The spermatheca proper is divided, by the attachment of the spermathecal duct, into a short basal section, and a longer U-shaped or J-shaped muscular section, respectively the collum and the cornua (Spett and Lewitt, 1926). The collum may be very small and bead-like or large and bulbous. The spermathecal gland, a nonsclerotized elongate sac, attaches to the apex of the collum. This accessory gland is sometimes damaged or difficult to find in preserved specimens, so that it is not always completely illustrated with the spermatheca, though at least the point of attachment is indicated. The muscles of the cornua extend from the apex across the curved portion. There is a closed nonsclerotized sac inside the cornua. Sperm that are forced into

the spermatheca partially collapse this internal sac. Contraction of the muscles extend the sac and force sperm through the spermathecal duct to the common oviduct. Care must be used in removing the spermatheca from the cavity of the abdomen or it will be broken. It is somewhat isolated from the other genitalic structures and often remains inside the abdomen when they are removed.

SEXUAL DIMORPHISM

The various characters exhibiting sexual dimorphism will be included with generic and specific treatments. The general dimorphic characters as well as those restricted to certain species will be pointed out for the North American species. When used alone these characters are diagnostic in most cases and when correlated with other characters, they are useful in showing the relationships of species within a genus. In some instances there is a continuum from one dimorphic character state to the other.

The most obvious sexually dimorphic characteristic of the group is size. Females are generally much larger than males, although the largest males of a species are the same size as or slightly larger than the smallest females. In a few cases the smallest female specimen may be similar in size to the smallest male, but never is the largest male as large as the largest female. This size difference is less obvious in the smaller species than in large ones.

Common to the entire group is a small to large midventral fovea on the last abdominal segment, especially of the female. There is considerable interspecific and some intraspecific variation among females in this character, but the fovea in the male is always smaller and less distinct than in the corresponding female. In most females it is a distinct, large, circular depression, whereas in the male the area is smooth and flat or only faintly impressed. In females this fovea is usually surrounded by long and short hairs, the longer ones covering the two sides and the short ones the anterior and posterior borders of the fovea. In males these hairs take the form of two groups on the foveal area separated by a shiny, smooth, or punctate section. Each group is usually made up of long anterior hairs gradually becoming shorter toward the posterior margin of the segment. Very short hairs are usually present along the margins of the foveal area.

Single or double apical spines occur on the front tibiae of most male chlamisines. An additional spine is found on the middle tibiae in some species or species groups. In females they may or may not be present depending upon the species group. Their arrangement in some species is the same in both sexes, but in most the females have none or fewer and smaller spines than in males. The number and sizes of tibial spines in each sex is usually constant for a given species, but in some there is variation.

Other kinds of sexual dimorphism restricted to certain genera, species or

species groups are found throughout the subfamily. Males of *Pseudochlamys* have enlarged and sometimes asymmetrical mandibles, while the females are normal. The head and pronotum of males also differ in size and shape from those of females in this genus.

Spines and spinulae as sexually dimorphic characters found on the ventral abdominal segments have already been discussed in my revision of *Exema* (Karren, 1966). These occur in some chlamisines but not in any of the species presently under consideration.

Several species of *Neochlamisus* have a wider prosternum in females than in males. In *N. gibbosus* and less so in a few other species, the prosternal process is strongly serrate in males and normally long and narrow in females. The pygidium in males is also elongate and narrowed at the apex in these same species. In some species, especially *gibbosus*, the abdominal process which partially covers the apex of each posterior femur is usually narrower and the sides more nearly parallel in females. There are differences in texture of the pygidium between males and females of *Neochlamisus,* but these are difficult to describe because of variation within species.

Only one species *(Chlamisus foveolatus)* shows any sexual dimorphism in color pattern, but it is so slight that it is of questionable value in distinguishing the sexes. The face of both sexes is partially yellow on the clypeus and lower frons. This coloring usually extends higher on the frons in males than in females. A much more striking characteristic is the wide prosternum and prosternal process found in females compared to the narrow subtriangular one in the males.

In *Chlamisus maculipes* the male antennae reach to the middle of the metasternum and have elongate segments. The female antennae barely reach the posterior margin of the prosternum. In addition, the prosternum and the metasternum between the coxae are covered with long dense hairs in the male, while in the female the hairs are short and scattered. The hairs on the prosternum of the male are decumbent, while those on the metasternum are erect.

A further discussion of sexual dimorphism in Neotropical species will be found in Monrós (1952).

INDIVIDUAL VARIATION

Moderate size and color variation among individuals is common in most species and is easily recognized. Size variation as sexual dimorphism was discussed in the previous section. Small color variations in the "metallic" species are very difficult to describe since changes in the direction of the light source can cause certain areas or spots to appear different. Occasionally major variation is related to the method of preservation or the

age of the specimens. Some variation may be due to the insects' having fed on different host plants, but there is no conclusive evidence of this. The extent of coloration in maculate species is subject to considerable variation, but the species can be recognized to some extent by coloration alone.

The tubercles and carinae follow the generalized pattern outlined for *Exema* (Karren, 1966), but it is difficult to describe accurately a particular tubercle or carina for a species because of extensive variation in sculpturing. The commonest condition is described for each species, and the reader is cautioned to realize that there may be considerable variation. A particular tubercle can be small or large, blunt or sharply carinate, and may be connected to another tubercle.

The pattern of punctures and foveae on two individuals is never exactly the same, although some specific uniformity can be found. For example, those in one species may be in general deeper, shallower, larger or smaller than those in a related species. When described as part of a complex of characters of a species, punctation can be used in specific differentiation. In a few species some variation has been found between males and females in the fovea on the last abdominal segment.

Intraspecific variation in the genitalia is usually very slight, while the genitalia of many closely related species are so similar that they are difficult to use in species diagnosis. An interesting exception has been studied by Brown (1944) in *Neochlamisus bebbianae*. He found a case of striking dimorphism in the male aedeagus in one population, the apex being either evenly rounded or bluntly pointed. In addition, differences were found in the ejaculatory guide and other sclerotized structures of the internal sac. An additional case of dimorphism of this type is found in *N. moestificus*.

Each species could be described as having characters varying normally. Most individuals of a species would fall fairly near the mean of variation of a character, but a few individuals with extreme conditions of the character under consideration might overlap with extreme individuals of another species. In a few cases I have been able to relate variation in a species to geographical distribution. This has been noted in the discussions.

In the descriptions, I have tried to describe for each character the commonest form, based on the available samples. Variation and exceptions are described in the discussions that accompany the descriptions. Accurate identification and understanding of the variability of a species is always easier when a large series is studied, especially when there are many individuals from one locality and preferably from one host.

LIFE HISTORIES

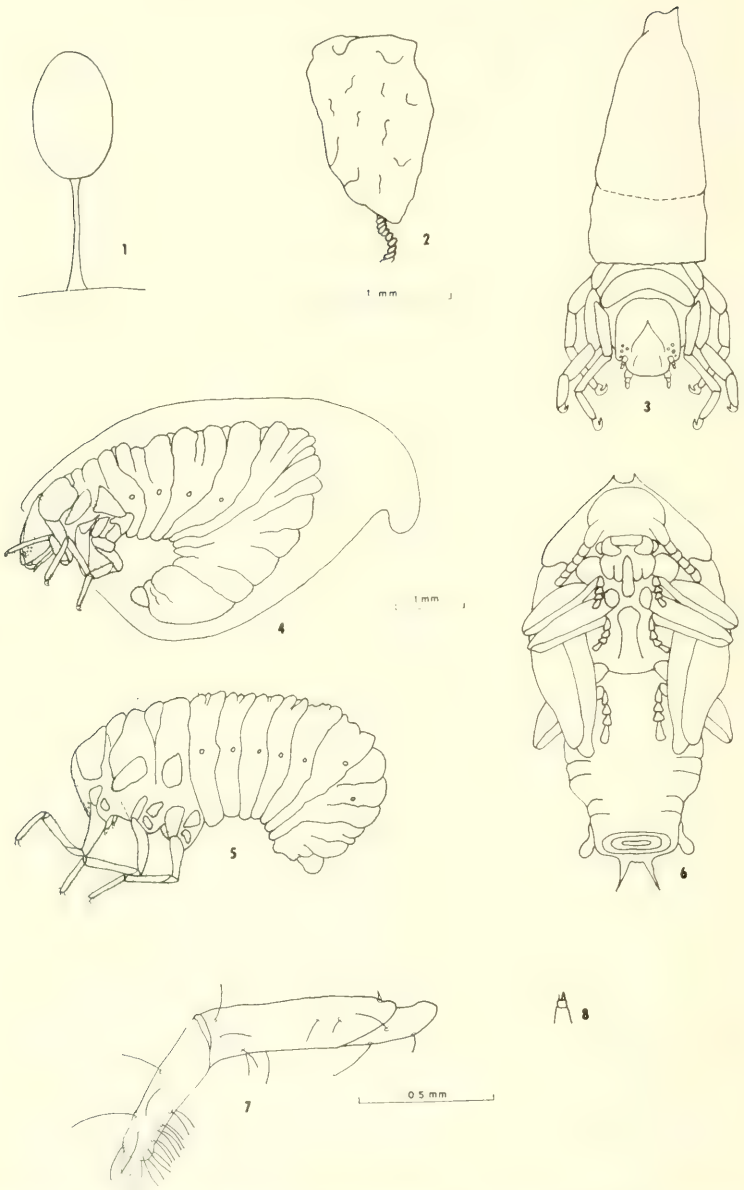
Life history studies have been investigated for species of the genera *Neochlamisus* and *Exema*. All species appear to have similar life histories

and case-bearing habits in the larvae. The same is true for the Neotropical species that have been studied. Each has a definite season of the year in which oviposition takes place. Short periods in which certain species can be taken in abundance and the simultaneous rarity of other species suggest that the season of adult activity for one species may be quite different from that of another in the tropics. Activity is probably correlated with growth and maturity of food plants. North American species are more similar in their seasonal activity, probably because climatic conditions to a certain degree correlate plant growth. Some seasonal differences in peak abundance have been noted for southern species which appear to have a more extended season of activity, and are found during the entire year.

The following information about life histories is taken from published data and from field and laboratory observations. Temperate North American species hibernate as adults and begin their egg laying in late April and early May. I have observed oviposition throughout the summer months in species of *Exema* in Kansas. Brown (1943) noted that the species he studied reached a peak of ovipositing the first week in June. One species in Kansas, *Neochlamisus platani,* is just beginning its egg laying in late May and early June. It can lay 10-15 eggs per day for short periods of time. Species of *Exema* lay only 1-3 eggs per day but may continue for a month in the laboratory.

Eggs are laid by first attaching a short stalk to the leaf. The female appears to use this stalk to pull the elongate yellowish or orange egg from the tip of the abdomen. The stalk is probably continuous with the chorion of the egg (Fig. 1). She then covers the eggs with her feces. Small flattened plates of greenish fecal material are squeezed between genital sclerites so that several are used to build the first row encircling the base of the egg. The stalk is twisted (Fig. 2) when the egg is rotated by the hind legs during this process. As one row is completed another is begun until the entire egg is covered and a flat top is added. Slight variations are found in the different species and genera. Shortly after the covering is completed the case hardens and turns a darker color. The process requires 15-20 minutes in the North American species that have been observed.

From six to ten days are required for the eggs to hatch. Humidity is an important factor in determining the hatching time in the laboratory. Upon hatching the larva chews away the flat top of the egg case. Contrary to my previously published observations (1964), the larva usually also chews away the end of the stalk inside the egg covering. The covering is then pulled away from the stalk and becomes the beginning of the larval case. Occasionally the larva leaves the case and chews away the stalk from the outside. During mid-summer, larvae of all stages can be taken on the host plants.



FIGS. 1-8. *Neochlamisus platani,* immature stages. **1,** egg on stalk; **2,** fecal covered egg; **3,** 2nd instar larva and additions to case; **4,** mature larva in case; **5,** prepupal stage; **6,** pupal stage; **7,** front leg of mature larva; **8,** antenna of mature larva. Upper scale Figures **1-3,** middle scale Figures **4-6,** lower scale Figures **7-8.**

The larva is somewhat U-shaped inside the case (Fig. 4). The legs are long and protrude from under the edge of the case (Fig. 3) as the larva moves over a surface. Feces, plant hairs, and other debris are used to enlarge the case. At each molt the case is attached firmly to the substrate for 1-2 days before the larva again begins to feed. The mature larva (Fig. 5, 7-8) also attaches its case firmly to the substrate before pupation (Fig. 6), usually in a protected area such as the axil of a leaf.

Late in the summer, adults begin to emerge from pupal cases that have been attached to plants for 2-3 weeks. The adults are fully colored and sclerotized, since they remain in the pupal case several days before emerging. There is apparently only one generation a year in the North American species. Adults collected early in the summer readily copulate, while those collected in August and September have never been so observed. More detailed information about specific life histories will be given, when available, with the species treatments.

Eggs, larvae and pupae collected in the field frequently produce parasitic Ichneumonidae, Chalcidoidea and Chalcididae. Available information on specific parasites is included in the species treatments.

Adult chlamisines are sometimes used to provision the nests of certain wasps of the genus *Cerceris*. Scullen (1965) cited two examples. The beetles have been identified as *Neochlamisus insularis* and *N. bebbianae*.

FOOD PLANTS

Earlier studies, especially by Brown (1943, 1946, 1952, 1961), indicated that most North American species have strong monophagous tendencies and limited geographic distributions. My studies have shown that distributions are much more extensive than was thought by Brown and that several food plants are used by some of the species. A few are generally monophagous throughout their range, but others are commonly found on several host plants. More complicated are those which occur on a particular host in one locality but a different host in another locality. In each genus or species group there seem to be species of each type.

Brown has published reliable host plant records for all the species included in his studies. To these, I have added a considerable number in this paper.

Previous to the work of Brown, a number of authors had reported host plants for several species usually under the names *Chlamys plicata* or *C. gibbosa*. Care must be used in referring to these records because of the previously confused nomenclature of the North American Chlamisinae.

Specimens are often taken on plants that are not used as food. Larvae especially wander to neighboring plants to pupate. The most reliable information comes from actual observation of feeding by adults and larvae or collection of a series of adults or larvae on the same plant. Food plants

from which a series of at least three specimens have been collected at one time and place are hereinafter identified with the word "series" in parentheses after the name of the plant. Those reported in the literature but not otherwise verified are identified with the word "literature" in the same manner. Plants on which larvae have been taken are also indicated.

SYSTEMATIC POSITION AND RELATIONSHIPS

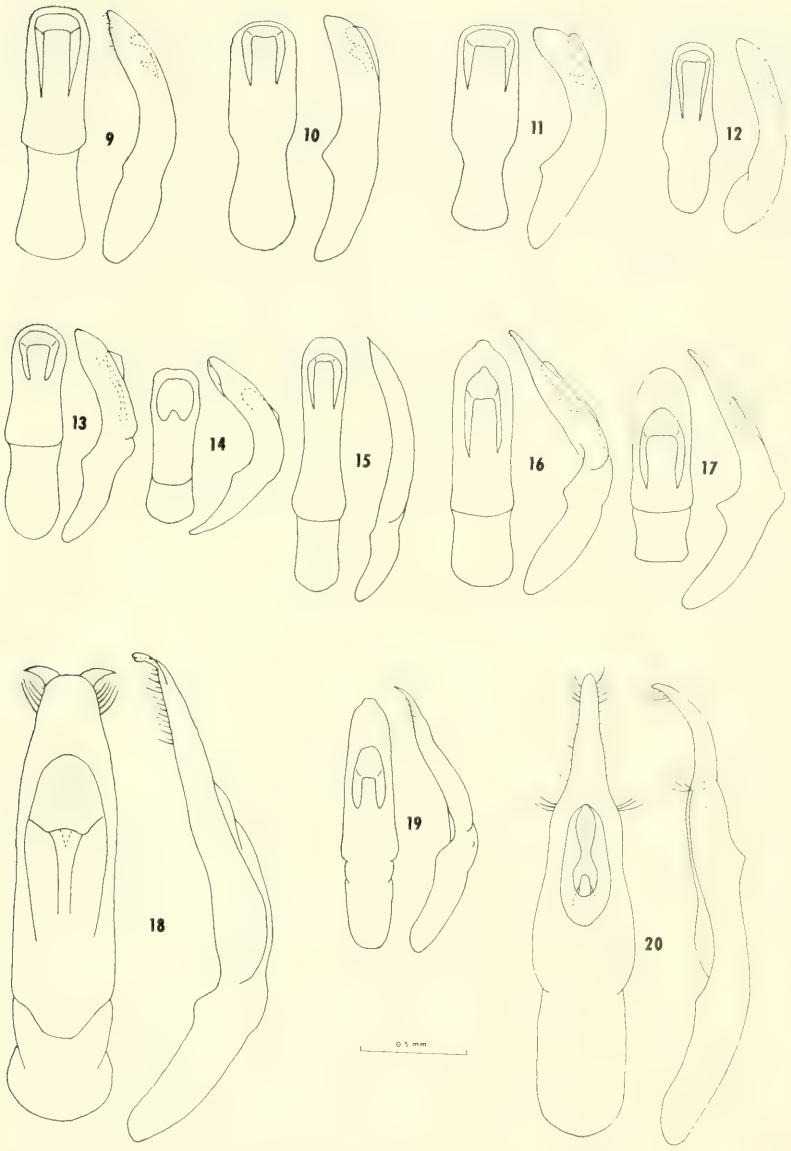
The systematic position of the subfamily has been discussed by several authors (Spett and Lewitt, 1926; Böving and Craighead, 1930-1931; Zia, 1936; Chen, 1940; Powell, 1941; Monrós, 1952; Varma, 1954, 1955; de Monte, 1957), using different bases, including female genitalia, male genital capsules, larvae, and wings. In general, they agree that Chlamisinae have definite affinities with the other camptosomates, those chrysomelids in which a larval case is constructed for all of the immature stages.

Many different opinions exist as to the taxonomic rank of the chlamisines. There has been a general tendency toward raising the taxon from tribe to subfamily to family. There are the usual advantages to retaining subfamily status for this group, as pointed out by Monrós (1952). I have followed his classification because it reflects more closely the present understanding of the phylogenetic relationship of the group to the rest of the chrysomelids.

For the most part, the elytral sculpturing is very distinctive for the group, but several Australian genera of Cryptocephalinae (*Brachycaulus, Lacnobothra,* etc.) have similar sculpturing. The enlarged asymmetrical mandibles in males of *Pseudochlamys* resemble those found in Clytrinae (Clytrini, Megalostomini). Although the adults of Lamprosominae differ in many respects from Chlamisinae, the larvae are very similar, and the lamprosomines are considered part of the camptosomates closely related to the Eumolpinae and Chlamisinae. They are intermediate in many respects between the two groups.

Powell's (1941) study of the male genitalia of chrysomelids showed a close relationship between the subfamilies Cryptocephalinae and Clytrinae. Powell was less certain about the relationship of the Chlamisinae to these two groups but believed that further study would prove their close relationship to Cryptocephalinae and Clytrinae. He examined only one species, *Exema dispar,* which proved to have several specializations. Powell used the presence of subapical hairs of the aedeagus, a characteristic found only in the camptosomates, to show the relationship of Chlamisinae to the other two subfamilies of the section. The Y-shaped spiculum gastrale and tegmen are found in many genera of Eumolpinae, Chrysomelinae, Donaciinae, Orsodacninae, and Criocerinae, but there is a closer similarity among those of the camptosomate genera studied by Powell.

Further study has indicated that the species of *Exema* found in North



Figs. **9-20.** Male aedeagus, dorsal and lateral aspects. **9,** *Pseudochlamys semirufescens;* **10,** *P. megalostomoides;* **11,** *Chlamisus flavidus;* **12,** *C. arizonensis,* **13,** *C. texanus;* **14,** *C. fovelatus;* **15,** *C. quadrilobatus;* **16,** *C. huachucae;* **17,** *C. nigromaculatus;* **18,** *C. maculipes;* **19,** *Diplacaspis prosternalis;* **20,** *D. paradoxa.*

America are some of the most specialized chlamisines with regard to the genitalia. The genus *Pseudochlamys* and some species of *Chlamisus* show a much closer relationship to the other camptosomates and better support the conclusions reached by Powell.

The terminal position of the apical orifice of the male aedeagus is a more generally occurring characteristic throughout the chrysomelids than the Y-shaped spiculum gastrale and tegmen. It is also found in most of the chlamisines that I have studied, however, as pointed out by Powell, its position is subcentral in *Exema*. I have also found this modified condition in many species groups of the chlamisines, including the genus *Neochlamisus*. This is interpreted as a specialized state. This characteristic, correlated with other morphological similarities between species, is one of the important criteria for the species groups treated in this paper.

SYSTEMATIC TREATMENT

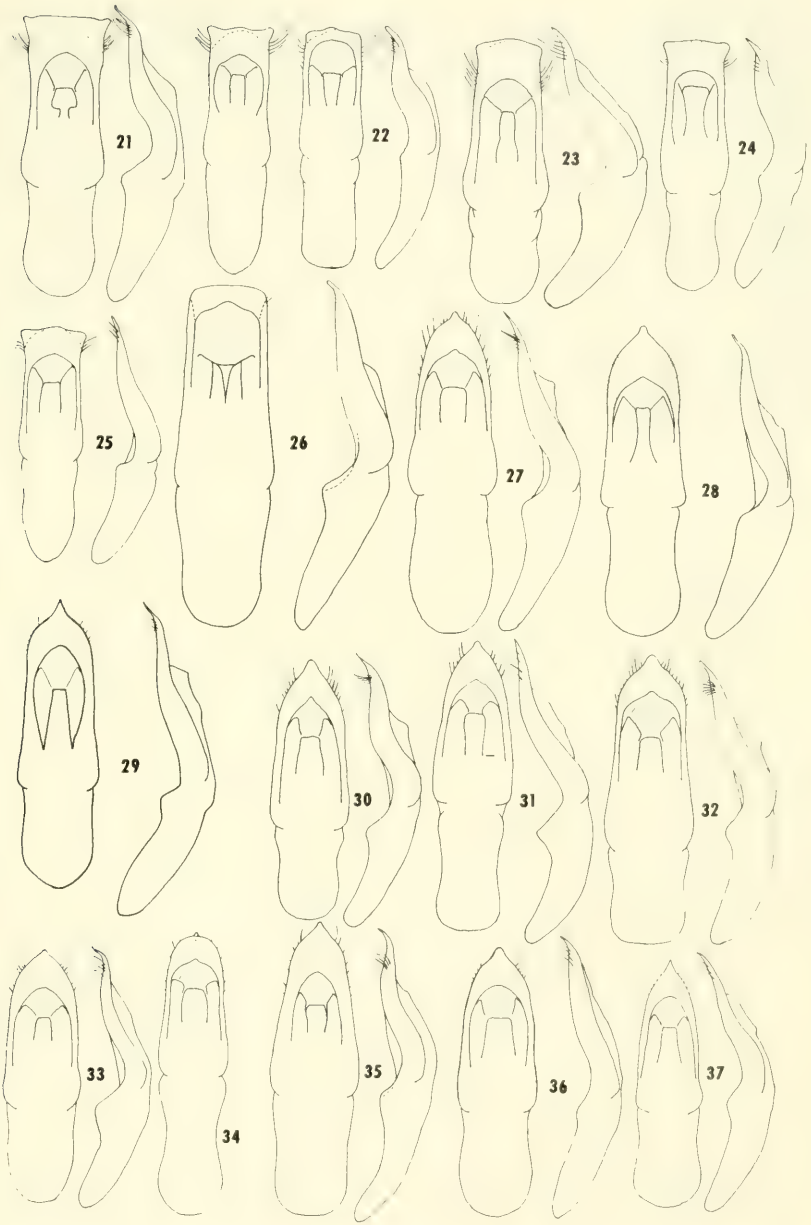
CHLAMISINAE Gressitt, 1946

Chlamydeae Lacordaire, 1848:636-643.
Chlamydae Baly, 1865:58.
Chlamydes Chapuis, 1874:193.
Chlamydinae Gemminger and Harold, 1874:3301.
Chlamydidae Jacoby, 1881:73-74.
Chlamydini LeConte and Horn, 1883:240-241.
Fulcidacina Jacobson, 1924:239.
Fulcidacinae Schaeffer, 1926:181-182.
Fulcidacini Leng and Mutchler, 1927:44, footnote 3.
Fulcidacidae Navajas, 1944a:75-76.
Chlamisinae Gressitt, 1946:84.
Chlamisidae Brues, Melander and Carpenter, 1954:577.

Type genus: *Chlamisus* Rafinesque, 1815 (=*Chlamys* Knoch, 1801, not Bolten, 1798). *Chlamys* is recognized as the type of the subfamily since Lacordaire (1848) used it as the basis of the family group name, Chlamydeae. The replacement name, *Chlamisus* becomes the type genus to retain the original application of the taxon. The name Fulcidacinae, based on the generic name *Fulcidax*, as proposed by Jacobson (1924) is invalid since it is not based on the valid name of the original nominal type genus.

REVIEW OF TAXONOMY

The chlamisine classification proposed by Lacordaire (1848) has been used by entomologists for over 120 years. It consisted of seven genera, with the large genus *Chlamys* divided into 14 species groups mainly on the basis of antennal form, body shape, and color. Although several authors have pointed out the shortcomings of this system, no one has attempted to completely revise Lacordaire's classification. During the years that Monrós worked with this group, he established two new genera for species that Lacordaire had included in *Chlamys* and *Exema*, leaving Lacordaire's basic



Figs. **21-37.** *Neochlamisus,* male aedeagus, dorsal and lateral aspects. **21,** *memnonius;* **22,** *moestificus* (dorsal aspects show extremes in variation); **23,** *velutinus;* **24,** *scabripennis;* **25,** *subelatus;* **26,** *gibbosus;* **27,** *bimaculatus;* **28,** *insularis;* **29,** *platani;* **30,** *bebbianae;* **31,** *eubati;* **32,** *fragariae;* **33,** *comptoniae;* **34,** *assimilis* (dorsal aspect only); **35,** *chamaedaphnes;* **36,** *cribripennis;* **37,** *tuberculatus.*

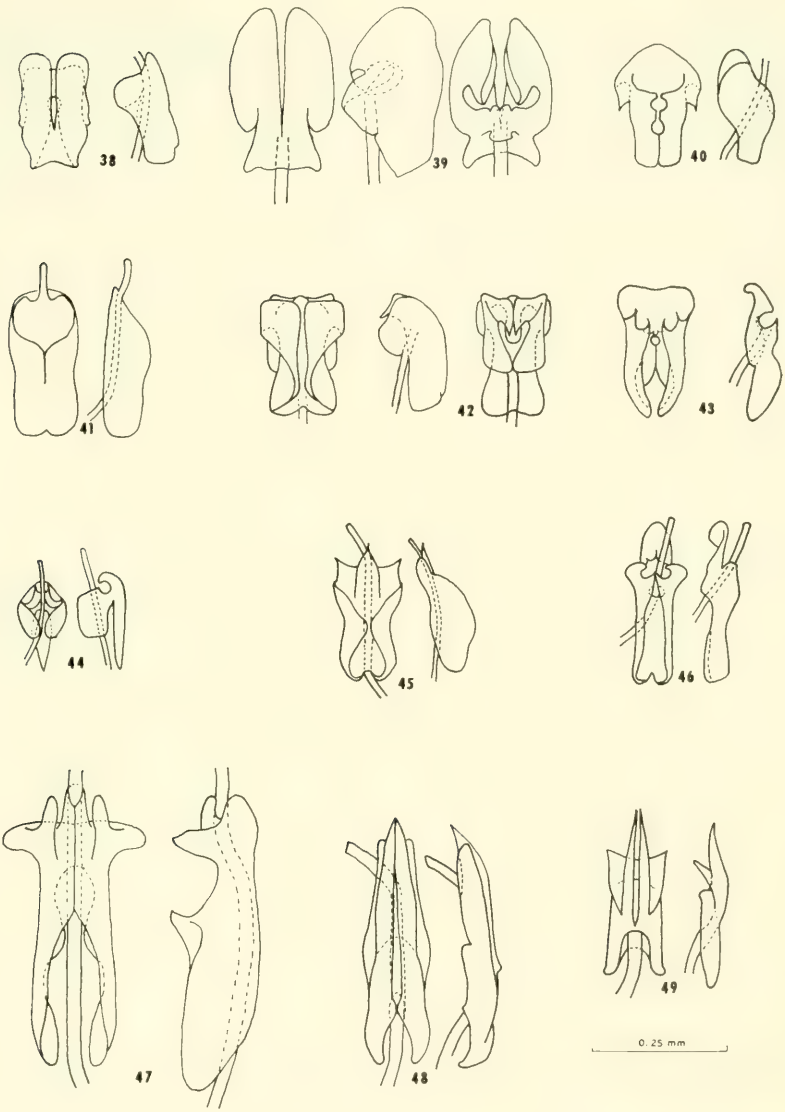
classification unchanged. As new species have been described, it has been found that the characters used by Lacordaire sometimes resulted in unrelated forms being placed close together in the classification. Additional difficulty has resulted because the descriptions and terminology were not always clearly understood.

A major problem with Lacordaire's classification is overlooked or disregarded characters. *Fulcidax* was characterized by having simple tarsal claws. Although this is a valid character for this genus, several species of North American *Exema* examined by Lacordaire also have the same condition. The one species of *Diplacaspis* was characterized by the unique metascutellum, although at least one species, and perhaps more, of *Chlamisus* examined by Lacordaire also have an exposed second scutellum. Less significant is the case of *Pseudochlamys,* which is characterized by large asymmetrical mandibles. A species of *Chlamisus* with similar mandibles was recognized by Lacordaire but thought to be a deformed specimen. Additional material and a study of the genitalia indicate that the mandibular condition in *Pseudochlamys* is more variable than originally supposed. Eventually several other species with buccal modification will be included in this genus.

The present revision includes all of the species found in America north of Mexico. Lacordaire's classification is followed where I feel it reflects the relationships of the species. A study of the male genitalia of North American as well as many Central and South American species indicates relationships among genera and species groups that are not evident in a study of antennae, body shape and color, upon which characters the classification of Chlamisinae had previously been based. It has been my purpose to show correlation of these characters with as many others as possible, especially the genitalia. The resulting classification probably reflects more closely the phylogenetic relationship of the groups within the subfamily.

Two related species groups formerly included in *Diplacaspis* and *Chlamisus* are found in North America; one is characterized by an exposed metascutellum and the other by a striate pronotum. Similarities in the male and female genitalia, antennae, and sculpturing suggest that the two groups are congeneric and a new genus *Neochlamisus* is proposed. Intermediate species and similar genitalic characters in the genus suggest species groups rather than subgeneric status for the two groups. It was felt that any other treatment of the species would be contrary to the present understanding of the relationships.

The metascutellum of *Neochlamisus* shows several degrees of exposure. It may be always broadly exposed, within a species, or variable from narrowly exposed, to rarely exposed, to never exposed. Exposure of the metascutellum is closely correlated in the *velutinus* species groups with the presence of two velvety spots on each elytron and single tibial spines in both



Figs. **38-49.** Male ejaculatory guide, dorsal and lateral aspects. **38,** *Pseudochlamys semirufescens;* **39,** *P. megalostomoides* (also ventral aspect); **40,** *Chlamisus flavidus;* **41,** *C. arizonensis;* **42,** *C. texanus* (also ventral aspect); **43,** *C. foveolatus;* **44,** *C. quadrilobatus;* **45,** *C. huachucae;* **46,** *C. nigromaculatus;* **47,** *C. maculipes;* **48,** *Diplacaspis paradoxa;* **49,** *D. prosternalis.*

sexes. The size of these spots also varies continuously from very large to absent. Both exposed metascutellum and velvety spots are found occasionally in the *gibbosus* group but never both in the same species.

The male and female genitalia respectively are more similar from species to species in *Neochlamisus* than in any other North American chlamisine genus. The specialized male structures are distinctive. The female spermatheca is similar throughout the genus and distinct from those of related genera.

The North American species left in *Chlamisus* belong to more than one genus according to the above standards, but until there has been further study of the Mexican species it is better not to propose new genera. It would be preferable to establish new genera when there is a clearer understanding of the included species and their taxonomic position in the subfamily.

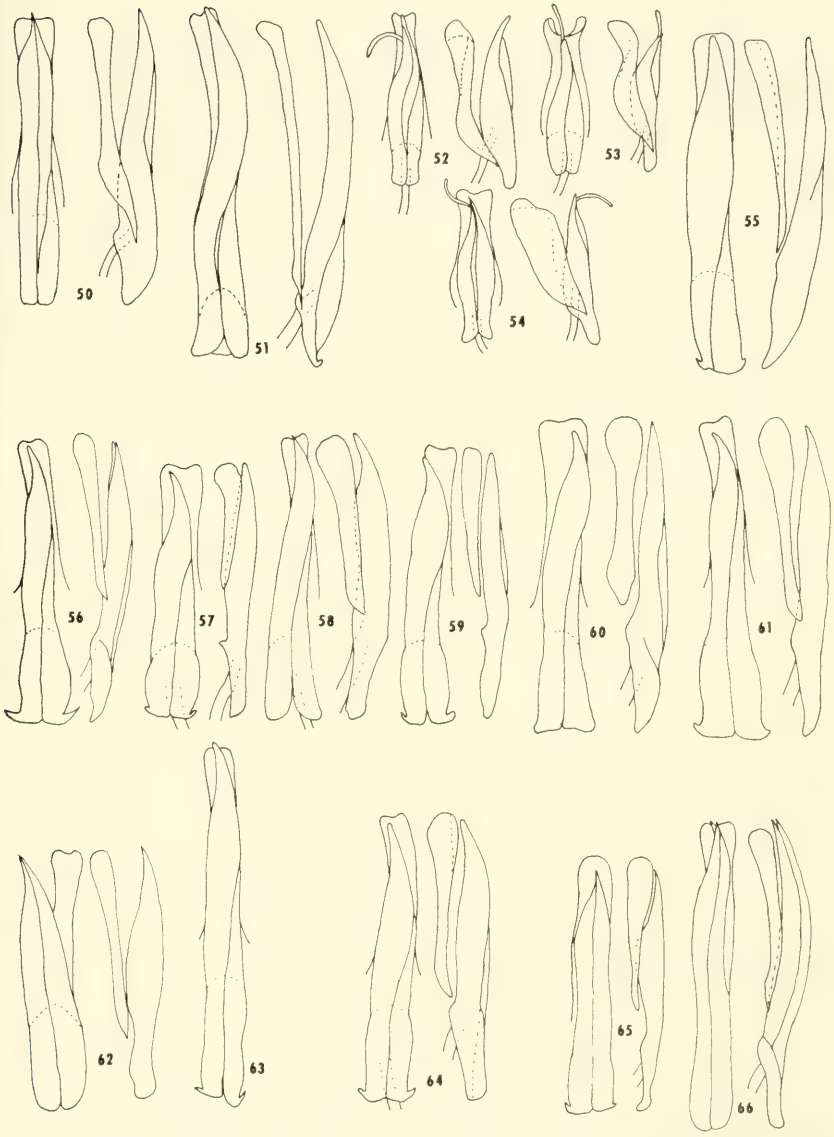
Pseudochlamys is represented by one new species in America north of Mexico. *Exema* has been treated previously (Karren, 1966). *Diplacaspis* is represented by one species quite different in shape and sculpturing from the type species, but the two have several characters in common including the genitalia that suggest the relationship. The male genitalia in species placed in *Diplacaspis* are less similar than those of species of *Neochlamisus* to which *Diplacaspis* is related, but several characters indicate relationship close enough for the species assigned to *Diplacaspis* to be included in the same genus as the type species. Several Neotropical species of *Diplacaspis* seem to be intermediate between the type species and the one species from our area.

I have been unable to associate two names proposed for North American species of Chlamisinae with any identified species. These are:

Chlamys tuberosa Knoch, 1801. Type locality: North America (probably Pennsylvania, since it came from Melsheimer's collection). Found on chinquapin (probably *Castanea pumila*). There are no other records of North American Chlamisinae on this plant, although several species have been found on related plants.

Chlamys polycocca Lacordaire, 1848. Type locality: United States. Lacordaire stated that his species was closely related to but distinct from his *plicata*. I am unable to recognize which one of the *gibbosus* group it is.

The published descriptions are inadequate, the type localities are too general, and no type specimens have been located. Both *tuberosa* and *polycocca* have for many years been considered synonyms or varieties of *gibbosus* (or *plicatus*) by most authors. The names *gibbosus* or *plicatus* have, however, been used for a number of closely related species for many years, so that the treatment of *tuberosa* and *polycocca* as synonyms of *gibbosus* is of questionable value. In the interest of stability and common usage I have not referred these names to any of the North American species.



Figs. **50-66.** *Neochlamisus,* male ejaculatory guide, dorsal and lateral aspects. **50,** *velutinus;* **51,** *memnonius;* **52,** *moestificus;* **53,** *scabripennis;* **54,** *subelatus;* **55,** *gibbosus;* **56,** *bimaculatus;* **57,** *insularis;* **58,** *platani;* **59,** *bebbianae;* **60,** *cubati;* **61,** *fragariae;* **62,** *comptoniae;* **63,** *assimilis* (dorsal aspect only); **64,** *chamaedaphnes;* **65,** *cribripennis;* **66,** *tuberculatus.*

KEY TO THE GENERA OF NORTH AMERICAN CHLAMISINAE

1a. Tarsal claws bifid (Fig. 126); prosternal process widened between mesocoxae; metascutellum broadly exposed ..... *Diplacaspis*
b. Tarsal claws simple or broadly toothed; sides of prosternal process parallel, convergent or serrate, if slightly widened between mesocoxae then metascutellum not exposed 2
2a. Mandibles of males enlarged, normal in female; prosternum strongly and abruptly constricted behind anterior margin, posternal process more than ¾ as long as prosternum ..... *Pseudochlamys*
b. Mandibles of males and females similar; prosternum gradually constricted behind anterior margin or prosternal process about ½ length of prosternum 3
3a. Male ejaculatory guide asymmetrical, with sheath; frons in emargination of eye with yellow spot (except *velutinus* which has two velvety spots on each elytron) ..... *Neochlamisus*
b. Male ejaculatory guide symmetrical, without sheath; frons in emargination of eye without yellow spot (face may be all or partly yellow, with yellow area extending into emargination, but elytra do not have velvety spots) 4
4a. Males with spines or spinulae on first ventral abdominal segment, sutural serration of elytra complete ..... *Exema*[2]
b. Males without spines or spinulae on first ventral abdominal segment, sutural serration of elytra incomplete, suture straight immediately behind mesoscutellum (except *quadrilobatus*) ..... *Chlamisus*

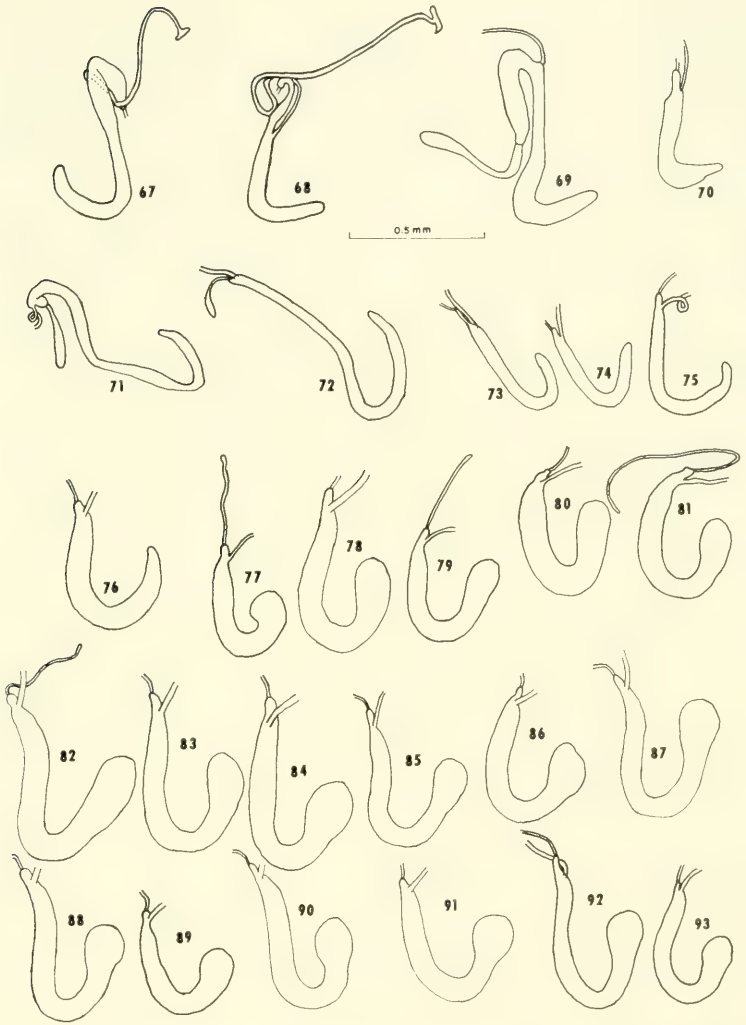
Pseudochlamys Lacordaire, 1848

Pseudochlamys Lacordaire, 1848:644.

Type species: Pseudochlamys megalostomoides Lacordaire (monotypic).

History: This genus was established by Lacordaire for a unique species with striking characteristics. Two more species were added when Bowditch (1913) transferred *Chlamys seminigra* Jacoby to the genus and described as new *P. rufescens*. At the time there was some doubt about the proper generic designation for both species. I have examined the type of *rufescens*, which is very similar to *megalostomoides*, and agree with those authors who place it in this genus. There has probably been some mistake concerning the drawing of *rufescens* supposedly made by Bowditch, in Achard (1914). It has very little resemblance to the specimens I have examined or to any other members of the genus. The specimens of *seminigra* in the Bowditch collection are congeneric with *Pseudochlamys*. The only other species described is *P. bellicosus* Monrós. At least two other species of *Chlamisus* that I have examined, from Mexico, probably should be placed in this genus, but definite action will not be taken until these species are studied further.

[2] Further treatment of *Exema* is excluded from this paper. For a revision of it see Karren, 1966.



Figs. **67-93.** Female spermatheca. **67,** *Pseudochlamys semirufescens;* **68,** *P. megalostomoides;* **69,** *Chlamisus flavidus;* **70,** *C. arizonensis;* **71,** *C. foveolatus;* **72,** *C. quadrilobatus;* **73,** *C. huachucae;* **74,** *C. nigromaculatus;* **75,** *C. maculipes;* **76,** *Diplacaspis prosternalis;* **77,** *Neochlamisus velutinus;* **78,** *N. memnonius;* **79,** *N. moestificus;* **80,** *N. scabripennis;* **81,** *N. subelatus;* **82,** *N. gibbosus;* **83,** *N. bimaculatus;* **84,** *N. insularis;* **85,** *N. platani;* **86,** *N. bebbianae;* **87,** *N. eubati;* **88,** *N. fragariae;* **89,** *N. comptoniae;* **90,** *N. assimilis;* **91,** *N. chamaedaphnes;* **92,** *N. cribripennis;* **93,** *N. tuberculatus.*

Diagnosis: The enlarged mandibles, genae and clypeus in males, shape of the prosternum, male and female genitalia and color pattern serve to identify this genus in North America.

Description: Males: 3.7-4.8 mm long; 2.1-3.0 mm wide. Females: 4.1-5.0 mm long; 2.4-3.0 mm wide. Coloration nonmetallic, yellowish or reddish brown with darker markings; underside and legs may be partially black.

Head enlarged or not, but usually visible from above (especially in males); pronounced sexual dimorphism: males with enlarged, sometimes asymmetrical mandibles, genae enlarged and elongated, clypeus enlarged and excavated; females more normal for subfamily, with very little enlargement of structures. First antennal segment (scape) in males sometimes enlarged and flattened, segment 2 (pedicel) subglobular, 3 smaller than 2 and subtriangular, 4 larger than 3 and subtriangular or subrectangular, 5-10 subrectangular, 11 subconical. Prothorax appearing reticulate, coarsely punctate with deep round punctures; evenly rounded or slightly gibbose, medial sulcus faint, carinae small or faint, tubercles absent, posterior lobes normal. Mesoscutellum normal, faintly granulate or shiny, concave or slightly carinate, posterolateral angles slightly reflexed (posterior elongations in *seminigra*). Metascutellum not exposed. Elytra moderately to coarsely punctate, tubercles and carinae faint or absent, with some of normal sculpturing visible. Pygidium moderately to coarsely punctate, nontuberculate and noncarinate, normal depressions faint, slightly convex. Prosternum expanded beneath enlarged mandibles in male, normal in female. Ventral thoracic segments foveolate, abdominal segments moderately to coarsely punctate, mid-ventral fovea of last segment small or absent in male, small to moderate in female. Tibial spines present or absent.

Aedeagus long and tubular, slightly curved, with apical orifice terminal; ejaculatory guide variable, in one piece, short, tubular. Spermatheca variable but usually long and slim without enlargements; duct not long and convoluted.

Distribution: This genus has been reported from Brazil, Paraguay, northeastern Argentina, Colombia, and Costa Rica. I have additional records from Panama, Honduras and southern Mexico. With the description of *P. semirufescens* n. sp. the distribution extends into the southern United States.

Systematic position: Many characteristics of the genus suggest that it is one of the more generalized of the subfamily. Species of this group have a definite affinity with the Clytrinae (especially Megalostomini) because of the similar sexually dimorphic characters. The poorly defined tubercles and carinae and absence of the pronotal gibbosity are generalized characteristics seen in closely related subfamilies. The female genitalia are of the generalized camptosomate type, while the male genitalia have many generalized characteristics found throughout the Chrysomelidae.

Discussion: Four species have already been described in this genus or referred to it: *megalostomoides, seminigra, rufescens,* and *bellicosus.* The only species found in North America is new and extends the distribution of the genus from southern Mexico into the southern United States.

The above generic description is based upon specimens of *megalostomoides* and *semirufescens* and information of other species given in the literature. Figures of *megalostomoides* are provided (Figs. 10, 39, 68) for comparison with those of *semirufescens.*

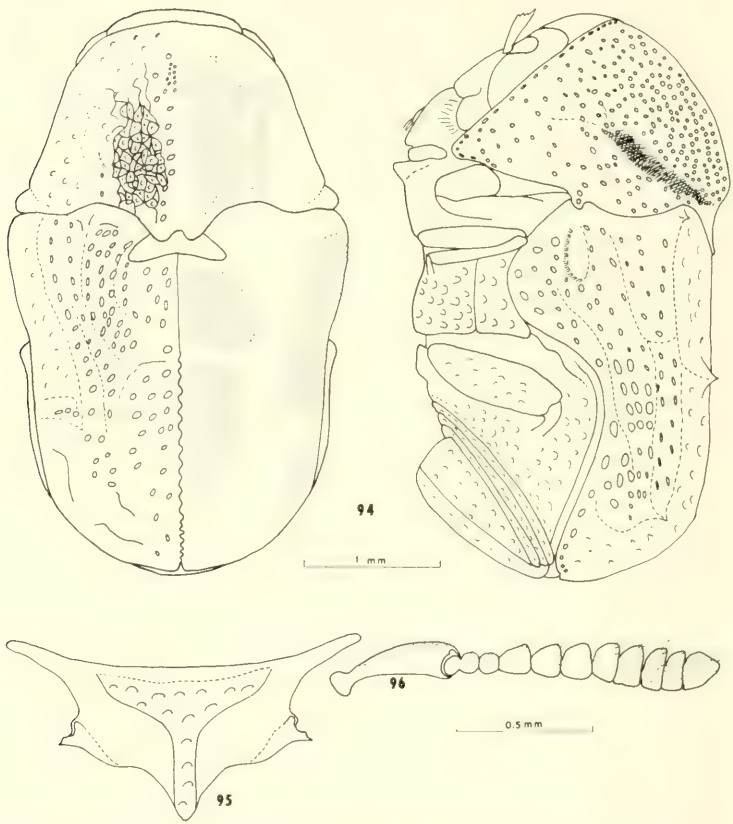
The taxonomic value of enlarged mandibles and other sexually dimorphic characters to identify members of this genus is not completely understood at this time. There are at least two Mexican species apparently of *Chlamisus* with enlarged mandibles, and further study may prove them to belong to *Pseudochlamys.* Several species of *Chlamisus* have many other characteristics similar to *Pseudochlamys,* but the males lack the enlarged mandibles. Many of the characteristics ascribed to *Pseudochlamys* by Lacordaire, Jacoby, Achard, and Monrós have already proven to be specific characters rather than generic ones. As further species of *Pseudochlamys* are described and the genus becomes better understood, its place in relation to other genera in the classification of Chlamisinae should become more evident.

Pseudochlamys semirufescens new species

Diagnosis: Since this is the only member of the genus in North America, it can be identified easily by the generic characteristics, and by the reddish brown markings on the yellowish dorsum. Both the male genitalia and female spermatheca are diagnostic for the species.

Description: Male holotype: 4.1 mm long; 2.4 mm wide. Color of dorsum yellow with two long, broad, reddish brown spots covering most of the pronotum leaving a central, longitudinal, narrow, yellow stripe, yellow anterior border and lateral spots; depressed areas of elytra including punctures reddish; vertex of head faintly reddish; mandibles dark brown; prosternal margins reddish; undersurface including legs mostly pale reddish with faint yellowish red areas; antennal segments 1-3 reddish, 4-6 yellow, 5 reddish, apical four segments dark brown; tarsal claws and tibial spines black.

Head moderately to coarsely punctate, punctures large and round; clypeus and genae tumid, less distinctly punctate than frons; mandibles large, mouthparts symmetrical; antennal segment 3 subtriangular and smaller than 2, 4 subtriangular with greatest width equal to width of following segments, 5-10 subrectangular, 11 subconical (Fig. 96). Pronotum coarsely and deeply punctate, gibbosity broad, faintly developed; tubercles and carinae absent; posterior lobes smooth. Mesoscutellum shiny, slightly concave, its posterolateral corners slightly reflexed, posterior margin con-



FIGS. **94-96.** *Pseudochlamys semirufescens.* **94,** dorsal and lateral aspects; **95,** prosternum; **96,** antenna. Upper scale Figure **94,** lower scale Figures **95-96.**

cave, anterior margin tuberculate, lateral margins slightly convergent. Elytra (Fig. 94) moderately to coarsely and deeply punctate, punctures round and setigerous; tubercles and carinae small or absent; small transverse su-2 carina joins long elevated area containing two subequal rows of punctures beginning at su-1a and extending to small su-3 tubercle; small submarginal carina extends from umbone to lateral area of su-3b, small carina extends from su-2a to submarginal carina; slightly depressed discal area, small areas anterior and posterior to su-2 depressed; anterior 1/2 of suture straight, posterior 4/5 serrate. Pygidium slightly convex, finely punctate, depressions faint, punctures round and deep. Prosternum (Fig. 95) broadly expanded behind mouthparts, sides strongly and abruptly convergent, process long and slim, about 3/4 as long as entire prosternum, apex curving toward base of metasternum, central area slightly depressed. First and last abdominal segments moderately punctate; small mid-ventral fovea on last

segment; foveal hairs few and scattered. Anterior and middle legs with small tibial spines.

Aedeagus (Fig. 9) short, curved, tubular, with fine scattered, lateral and ventral hairs near apex, apical orifice subterminal; ejaculatory guide (Fig. 38) short and tubular.

Female allotype: 4.3 mm long; 2.5 mm wide. Similar to male except mandible small as in other chlamisines; mid-ventral fovea of last abdominal segment larger than in male and with many hairs; no tibial spines; antennal segment 7 yellow, 8 light brown, 9-11 dark brown.

Spermatheca (Fig. 67) irregularly S-shaped, cornua evenly tubular to apex, apical 1/2 uniformly curved; collum suddenly recurved and expanded before apex; spermathecal duct short and explanate at attachment to common oviduct.

Types: Male holotype, Arivaca (Pima Co.), Arizona, 26 July 1941, E. L. Todd; female allotype, same locality and date, R. H. Beamer (both UK). Paratypes, all 17 from Arizona: 2♂, Arivaca, Pima Co., 14 July 1966, A. G. Hamilton, grass and mesquite, (JBK); 1♂ & 2♀, Patagonia Mts. (Santa Cruz Co.), 15 July 1952, 20 Aug. 1940, 4 Aug. 1953, D. J. & J. N. Knull (OSU, JAW); 1♀, Patagonia (Santa Cruz Co.), 29 July 1945, F. H. Parker (UAR); 1♂ & 1 ♀, Santa Rita Mts. (Pima Co.), 12 June 1933, R. H. Beamer (UK); 1♀, same locality, July, F. H. Snow (UK); 1♀, same locality, June, D. K. Duncan (UAR); 1♂, Oak Creek Canyon (Coconino Co.), 9 July 1941, L. H. Banker (UK); 1♂, Baboquivari Mts. (Pima Co.), F. H. Snow (UK); 1♂, same locality, 8 July 1935, E. D. Ball (UAR); 1♂, Globe (Gila Co.), 15 July 1943, F. H. Parker (UAR); 1♀, Santa Catalina Mts., Pepper Sauce Canyon (Pima Co.), 16 Aug. 1924, E. P. Van Duzee (USNM); 1♀, Nogales (Santa Cruz Co.), 25 June 1933, J. Russell (UK); 1♀, same locality, Sept., A. Koebele (CAS). (Map 1.)

Discussion: The type and paratypes were the only specimens available for study, except 1♂ and 1♀ in the Fall Collection (MCZ) (Santa Rita Mts., July, F. H. Snow). They are labeled *Chlamys arizonensis* Linell. The name *semirufescens* describes the reddish markings of the beetle.

In shape, sculpturing and color pattern, this species has many similarities to *megalostomoides*. The most striking similarity is in the females; the males of *semirufescens* appear to be specimens of *megalostomoides* with poorly developed mandibles and a slightly excavated clypeus. Characters differentiating the two species are found in the male and female genitalia.

Specimens of *megalostomoides* were thought to be very uncommon until recently. Recognition of the host plant and additional collecting reveals that they are common from southern Brazil to southern Mexico on *Waltheria americana* and possibly one other species of *Waltheria* in Brazil (Bokermann, in correspondence). The strict monophagy observed for this species may be some indication of a similar relationship of *semirufescens* to its possible food plant.

This beetle has been misidentified as *Chlamisus arizonensis* in most of the borrowed material. The superficial similarity of *semirufescens* to the pale species of *Chlamisus* has also caused some confusion of it with those species, but the male and female genitalia are quite different in each species.

A close examination of the size, shape, sculpturing and coloration also furnishes numerous characters for distinguishing *semirufescens* from the pale species of *Chlamisus*, even if males are not available or the genitalia are not examined.

The small number of specimens available from a limited area reveals less variation than is normally found in species of the subfamily. Individuals vary in the darkness of the color markings but not in the pattern. There is little variation in size, even between sexes, among the specimens examined.

There are no host data for this species except a vague record of two specimens collected by A. G. Hamilton from sweepings of "grass and mesquite."

Chlamisus Rafinesque, 1815

Chlamys Knoch, 1801:122-128 (not Bolten, 1798[3]).
Chlamisus Rafinesque, 1815:116.
Arthrochlamys H. Ihering,[4] 1905:642.
Boloschesis Jacobson, 1924:239.
Bolochesis Leonard, 1928:463, footnote 55a (misspelling).

Type species: Chlamys foveolata Knoch, designated by Navajas, 1946. Navajas did not select *tuberosa*, the first species described by Knoch as the type species because there is a question about its identity. Two other species, *Clythra monstrosa* Fabr. and *Bruchus gibbosus* Fabr. had been designated earlier as types of the genus, but are invalid because neither was an originally included species.

History: Chlamys was generally recognized as the valid name of the genus for about 130 years, during which time nearly 400 new species were described. Three authors during this period discovered that *Chlamys* was a junior homonym of *Chlamys* Bolten (1798), a mollusk (available according to Opinion 96 of the International Commission on Zoological Nomenclature).

Boloschesis, the youngest of the synonyms of *Chlamys* Knoch, was the first name used in a major revision (Schaeffer, 1926). Brown (1943), in his revision of the Canadian species, recognized *Arthrochlamys* as the valid

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[3] Sometimes listed as Röding or Bolten in Röding, 1798. The homonyms listed in Neave, 1939, p. 703, are as follows:
"*Chlamys* Bolten 1798, Mus. Bolten., 2, 161.—Moll. Cf. *Myochlamys* Ihering 1907.
Chlamys Knoch 1801, N. Beitr. Insectenkunde, (I) 122.—Col. (See *Arthrochlamys* Ihering 1904 & *Boloschesis* Jacobson 1942).
Chlamys Young & Young 1877, Ann. Mag. nat. Hist., (4) 20, 429.—Spong.
Chlamys Beneden 1892, Bull. Acad. Sci. Belgique, (3) 23, 227.—Crust."

[4] Sometimes listed as Ihering and Ihering. Although they coauthored the article, the authorship of the new names is clearly stated on page 679.

name. The oldest available name, *Chlamisus,* was not used until 1946 by Gressitt. Neave (1939), previously recognized the name *Chlamisus* Rafinesque (1815), and incorrectly stated that it was an emendation of *Chlamys* Berthold (1827); however, Berthold was presumably merely using Knoch's name of 1801.

It is not entirely clear that Rafinesque (1815) was proposing *Chlamisus* as a substitute name for *Chlamys.* Other genera of Chrysomelidae for which Rafinesque appears to have proposed replacement names in the same manner have been entirely overlooked by subsequent authors. They are not even recognized as junior synonyms as far as I can determine. Nevertheless, I am accepting *Chlamisus* Rafinesque as a replacement name for *Chlamys* Knoch (1801). *Chlamisus* has been generally accepted since Gressitt (1946) used it as the valid name for the largest chlamisine generic group.

In 1940 and 1942, Chûjô synonymized the name *Chlamys* under *Exema* because of the difficulty in separating these taxa using Lacordaire's key. He later (1955, 1956) recognized the validity of *Chlamisus* but retained his concept of one taxon for the two genera. In these same papers he listed *Myochlamys* Ihering, 1905 (this should be 1907) as a synonym of *Chlamisus* or *Exema,* but *Myochlamys* was proposed as a replacement name for *Chlamys* Bolten in Mollusca and should not appear as a synonym of any coleopterous group.

The name *Chlamisus* has been used for over 450 of the 577 species of the subfamily. In many respects it has been a "catch-all" genus rather than a clearly defined morphological taxon. I have used the name *Chlamisus* in a provisional sense pending revision of the Neotropical fauna. In this study, the genus includes those species of North America still remaining in *Chlamisus* after removal of the *gibbosus* species group. The reasons for this change are given in the treatment of *Neochlamisus,* new genus. The eight species that remain clearly represent two distinct lines of evolution on the basis of male genitalia. Numerous other differences characterize these species so that there is very little difficulty in identifying them. General statements about the genus are difficult. It is especially difficult to make a description of the genus that will apply to all the included species. The following diagnosis and description are based only on the known North American species now included in *Chlamisus.*

Diagnosis: The presence of a tibial spine on the front legs and sometimes middle legs of males, lack of any tibial spines in females, and absence of the diagnostic characters of the other genera serve to distinguish the *Chlamisus* in North America.

Description: Males: 2.5-6.0 mm long; 1.4-3.9 mm wide. Females: 2.6-6.0 mm long; 1.5-4.1 mm wide. Color varying from yellow with dark markings

to slightly metallic black; underside and legs completely or in part dark brown.

Head finely to coarsely and deeply punctate, usually depressed or grooved on upper frons; antennae variable. Pronotum finely to coarsely and deeply punctate, often reticulate, gibbosity slightly developed and faintly divided to large and deeply divided; nontuberculate or with rounded tubercles and carinae. Mesoscutellum subquadrate, granulate to striate or carinate. Elytra moderately to coarsely punctate, with small to large tubercles and carinae; anterior suture usually straight (serrate in *quadrilobatus*), posterior suture serrate. Pygidium convex, surface evenly rounded or tuberculate, medial carina present or absent. Prosternum subtriangular to goblet-shaped, coarsely punctate, concave or slightly convex. First abdominal segment punctate, foveolate, carinate or reticulate; last abdominal segment moderately or coarsely punctate or foveolate; mid-ventral area flat to deeply foveolate with surrounding foveal hairs. One tibial spine on front and sometimes middle legs of male, no tibial spines in female.

Aedeagus variable; long, curved, tubular, with blunt or rounded apex, to flattened and explanate, with or without apical hairs; apical orifice terminal or subcentral; ejaculatory guide tubular, variable, diagnostic for each species, never with a sheath; dorsal wall of internal sac with curved, sclerotized hook. Spermatheca variable, diagnostic for each species.

Distribution: The genus *Chlamisus* as presently understood is found in all zoogeographical realms, but only in extreme southern and eastern parts of the Palearctic and the northern tip of Australia. It is most abundant in the Neotropical realm. In North America it is found from the extreme Southwest to the southern New England states.

Systematic position: Chlamisus as treated here includes a few species which resemble *Pseudochlamys,* a few which share characteristics with *Diplacaspis* and *Neochlamisus,* and a few intermediates. The genus in North America is much more variable than any of the other genera and its species show a continuous spectrum of variation in several characters between *Pseudochlamys* and *Diplacaspis.* An example of this is the apical, subapical, or subcentral position of the apical orifice of the aedeagus. The loss of apical hairs on the aedeagus in a few species is a specialized condition; apical hairs are present in most camptosomates.

Discussion: Further study of the numerous Mexican and Neotropical species of *Chlamisus* will probably prove the North American species to be northern representatives of several generic groups. The present evidence indicates that North American species are products of specialization at the fringe of chlamisine radiation. Additional information is needed especially about Neotropical species groups and their relationships before a more meaningful classification can be proposed for the present genus *Chlamisus.*

As this knowledge is obtained, new genera will be named for species groups that deserve generic status.

Lacordaire's groups do not seem to reflect the phylogenetic relationships between groups. A preliminary examination of examples from most of his species groups shows that some species of each group have similar genitalia, supporting the other group characters, but a few forms exist that are poorly associated under his groups. Further study is needed to determine the relationship of species within each group and the phylogenetic relationship of the groups.

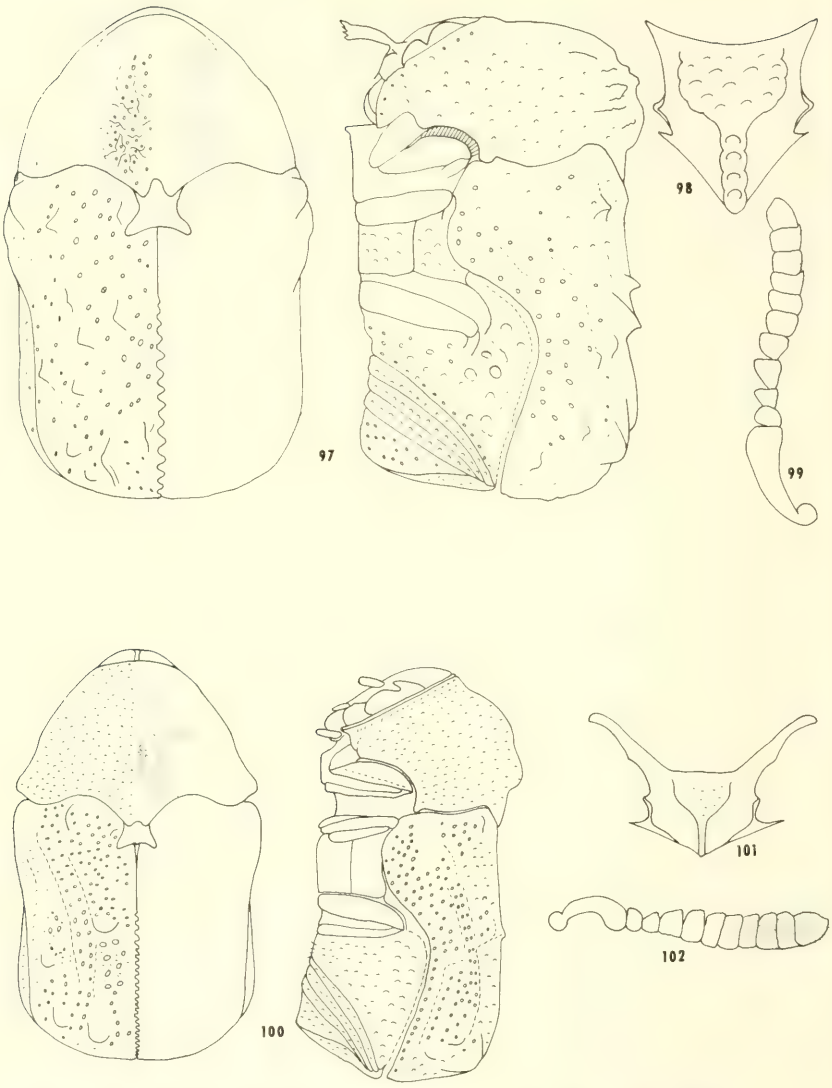
Key to the North American Species of *Chlamisus*

1a. Pronotum and elytra pubescent ..... *maculipes*
b. Pronotum and elytra glabrous 2
2a. Elytra uniformly black 3
b. Elytra pale with reddish brown markings 4
3a. Head in part yellow; pronotum coarsely punctate ..... *foveolatus*
b. Head entirely black; pronotum tuberculate and finely striate .... *quadrilobatus*
4a. Posterolateral slopes of pronotum striopunctate; upper frons with wide, black inverted V; pronotum and elytra with extensive black markings ..... *nigromaculatus* n. sp.
b. Posterolateral slopes of pronotum not striopunctate; head yellow with pale or small dark spot or stripe on upper frons; pronotum and elytra with pale markings 5
5a. Pronotal gibbosity not divided; pygidium finely or moderately punctate on basal half 6
b. Pronotal gibbosity faintly divided; pygidium coarsely punctate on basal half 7
6a. Head deeply punctate; elytra faintly tuberculate, with small irregular longitudinal carinae ..... *arizonensis*
b. Head not deeply punctate; elytra with large rounded tubercles .. *flavidus* n. sp.
7a. Pygidium coarsely punctate at base to finely punctate at apex, punctures deep; apical 1-2 segments of antennae dark brown; pronotum and elytra yellow to reddish brown with irregular dark markings ..... *huachucae*
b. Pygidium coarsely, deeply and evenly punctate, reticulate; apical 5-6 segments of antennae dark brown; pronotum yellowish green; elytra pale with large dark spot near scutellum ..... *texanus*

Chlamisus flavidus new species

Diagnosis: The pale color and dark markings, large and rounded tubercles on the elytra, punctation of the head, pronotum and pygidium are distinctive features of this species. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male holotype: 3.3 mm long; 2.3 mm wide. Color yellow with black to light brown markings; antennae mostly yellow, gradually



FIGS. 97-99. *Chlamisus flavidus*. **97,** dorsal and lateral aspects; **98,** prosternum; **99,** antenna. FIGS. 100-102. *Chlamisus arizonensis*. **100,** dorsal and lateral aspects; **101,** prosternum; **102,** antenna.

becoming light brown on apical seven segments; faint brown spot on center of vertex; pronotum with irregular light brown area extending along lateral slopes of gibbosity, becoming darker on posterior slopes; posterior margin of pronotum and anterior margins of elytra brown to black; prosternum with light brown to black margins, center of metasternum light

brown, anterior processes black; posterior margins of abdominal segments light brown; small central area of each leg segment light brown.

Head coarsely punctate, less so on upper frons; antennal segment 3 subtriangular, 4 subrectangular, 5-10 rectangular (Fig. 99). Pronotum moderately and deeply punctate, with coarse depressed punctures on gibbosity, tubercles absent; gibbosity not divided, evenly rounded, posterolateral slopes deeply punctate, posterior lobes smooth, tumid. Mesoscutellum carinate, posterior margin slightly depressed and emarginate, sides convergent anteriorly, posterolateral corners slightly reflexed. Elytra (Fig. 97) with large rounded tubercles, ae, su-1, su-1a, su-2a, su-2b, su-3, su-3a and ap; sc small, others faint or absent; su-1 posterior to normal position; suture closed anteriorly, posterior 3/4 serrate. Pygidium moderately punctate, depressions faint. Prosternum (Fig. 98) about twice as long as wide, central area slightly depressed. First abdominal segment roughly foveolate, last segment finely punctate, with small mid-ventral fovea on its posterior half. Well developed tibial spine on front and middle legs.

Aedeagus (Fig. 11) tubular, curved, sides constricted before middle, with fine apical hairs; apical orifice subterminal; median dorsal plate wide; ejaculatory guide (Fig. 40) tubular, with anterior enlargement below orifice, slightly narrowed behind.

Female allotype: 3.8 mm long; 2.6 mm wide. Coloring and sculpturing as in male except short dark stripe on center of vertex, posterior slopes of pronotal gibbosity darker than in male. (Scutellar angle of left elytron incompletely formed in this individual.) Large, deep mid-ventral fovea on last abdominal segment. No tibial spines. Spermatheca (Fig. 69) long, S-shaped; base of cornua long and straight, apical one-third slightly enlarged; collum half as long as cornua, slightly enlarged and recurved next to base of cornua; duct long and coiled, not convoluted; spermathecal gland sac-like, as long as collum.

Types: Male holotype, Hermosillo, Sonora, Mexico, 18 June 1961 (KU); female allotype and 1 ♂ paratype, Arizona, Andreas Bolter Collection (INHS, UK). Three additional paratypes from Sonora, Mexico: 1 ♂, Guaymas, 3 June 1967, on *Larrea divaricata* (JBK); 2 ♀, Huatabampo, 29 May 1955, F. Pacheco (ENA). (Map 1.)

Discussion: The genitalia of *flavidus* have several similarities to those of *Pseudochlamys semirufescens,* including the curved, tubular aedeagus, the subterminal apical orifice, the tubular ejaculatory guide and irregular, S-shaped spermatheca. However, the genitalia are more similar to those of several other species of *Chlamisus.* This species has been placed with the species of *Chlamisus* also because of the small mandibles in the males and the similar sculpturing.

The host plant of *flavidus* is uncertain since there has been a plant associate reported for only one specimen, taken on *Larrea divaricata.* Only the six types were available for study.

Chlamisus arizonensis (Linell)

Chlamys arizonensis Linell, 1898:479-480.
Chlamisus arizonensis (Linell); Monrós, 1954:24.

Diagnosis: This species is characterized by an elongate form, coarse and deep punctations, head and pronotum faintly tuberculate, elytra with small irregular carinae, and moderately, evenly punctate pygidium. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male: 3.2-3.3 mm long; 1.7-1.8 mm wide. Female: 3.5-3.8 mm long; 2.0-2.1 mm wide. Color yellowish brown with light brown to black markings, head with dark stripe or spot on upper frons; apical 4-5 antennal segments dark; pronotum with black spot on top of anterior slope, upper sides of gibbosity darkened by large Y-shaped band extending back over posterolateral slopes to posterior margin, small dark area anterior to ae tubercle; posterior margin of pronotum and anterior margins of elytra black; central area of sterna brown to black; anterior margin of prosternum black, sides brown.

Head coarsely and deeply punctate; antennal segment 3 subtriangular, 4-10 rectangular (Fig. 102). Pronotum coarsely and deeply punctate, punctures depressed and evenly distributed; gibbosity rounded, not divided; posterior lobes small. Mesoscutellum slightly convex, posterior margin depressed and broadly emarginate, sides slightly convergent anteriorly, posterolateral angles acute. Elytra (Fig. 100) faintly tuberculate, ae small, su-2 and su-3 small and broad; faint, irregular, longitudinal carinae separated by large, deep and depressed punctures; discal depression distinct, small depression with 4-7 punctures posterior to su-2; anterior elytral suture closed, posterior 3/4 serrate. Pygidium moderately and evenly punctate, depressions faint, carinae lacking. Prosternum (Fig. 101) less than twice as long as wide, sides slightly emarginate, gradually converging to apex of process; central area depressed. First abdominal segment rough, moderately punctate; last segment coarsely punctate medially to finely punctate laterally; large shallow mid-ventral fovea in both sexes, lateral hairs short in male, long in female; mid-ventral margin of segments 1-4 with long hairs in both sexes. Tibial spine on front and middle legs of male; no tibial spines on female.

Aedeagus (Fig. 12) enlarged before middle, curved and tubular, with no apparent apical hairs; apical orifice subterminal; median dorsal plate wide; ejaculatory guide (Fig. 41) tubular with medial anterior projection. Spermatheca (Fig. 70) L-shaped, cornua narrowed at apex, collum about twice as long as wide, length equal to width of cornua.

Types: Linell described *arizonensis* from two females collected in Arizona by Morrison, one from the Riley collection, the other from the Hubbard and Schwarz collection. Both of these are in the United States

National Museum type collection (USNM, no. 1298). The former is here designated the lectotype. H. S. Barber (unpublished) considered these specimens holotype and paratype respectively. According to the type label, Linell named this second specimen after Morrison, the collector of the specimens; but the name was never published. He must have changed the name after returning the specimens to Schwarz.

Discussion: It was necessary to examine the two type specimens of *arizonensis* to distinguish it from several other species in the Southwest with which it has been confused. Two misidentified specimens in the Fall collection (MCZ) are *P. semirufescens.* Borrowed collections contained six species under the name *arizonensis.* Monrós (1954), after examining the types of *arizonensis* and *huachucae,* synonymized the two, but a study of additional specimens and the male and female genitalia of the two forms indicates two species.

Specimens examined (6 males and 10 females): (Map 1)
UNITED STATES: ARIZONA: Cochise Co., 14 June, 8-20 July, 7 Aug.; "Granite Dell," 11 July.

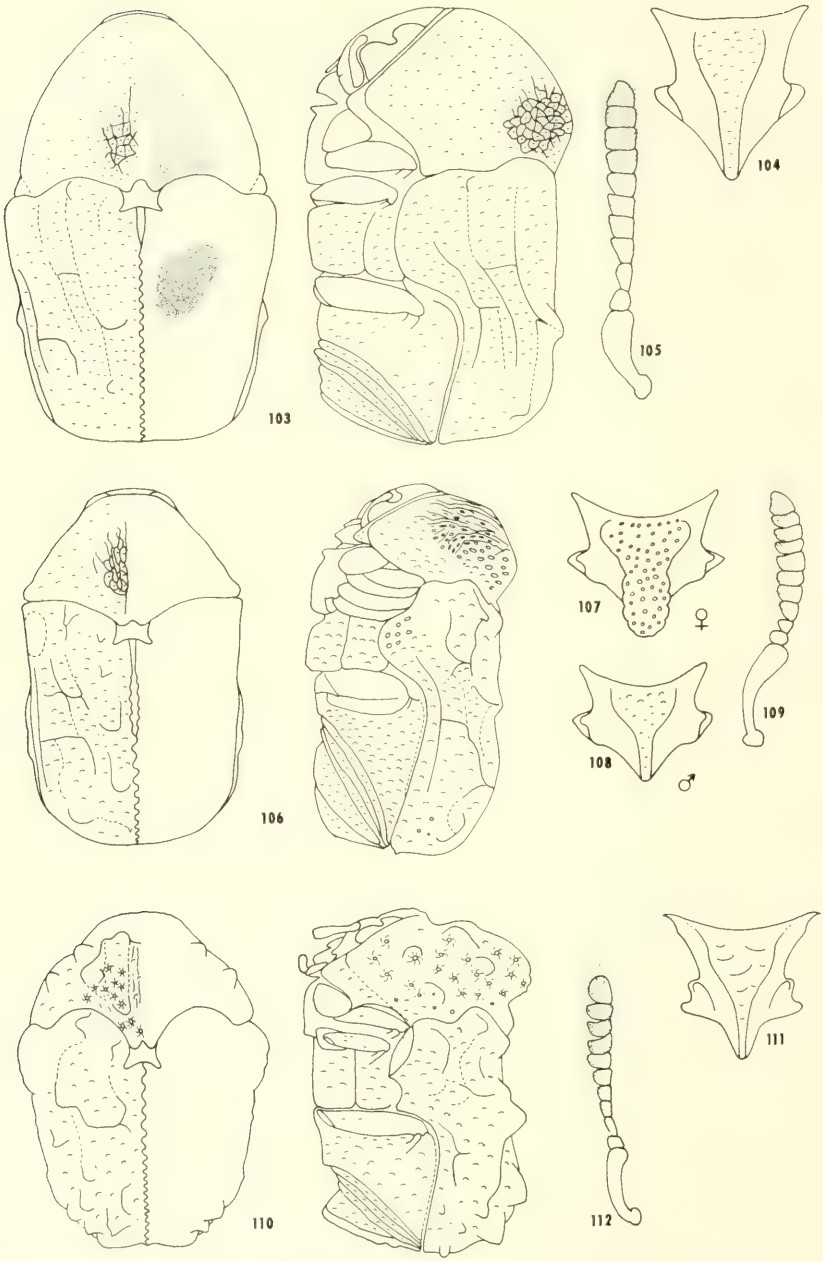
Chlamisus texanus (Schaeffer)

Chlamys texana Schaeffer, 1906:227-228.

Diagnosis: The unusual greenish coloration, large markings and small carinae on the elytra, and dark brown five or six apical segments of the antennae will identify this species. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male (based on the type and one other male specimen, both in the United States National Museum): 3.2 mm long; 2.1 mm wide. Head reddish brown, yellow between bases of antennae, dark spot on middle of vertex; antennae light brown, apical 5-6 segments dark brown; yellowish green pronotum marked on posterolateral slopes with reddish brown spot joined to light brown arch across anterior summit; posterior margin of pronotum and anterior margin of elytra black. Elytra yellow to light brown, each with large dark reddish brown spot anterior to su-2 tubercle. Pygidium greenish yellow; prosternum yellow with light brown margins; metasternum dark brown, becoming lighter brown laterally; ventral abdominal segments light brown, becoming greenish yellow laterally.

Head moderately and deeply punctate, lower frons and clypeus with recessed punctures producing a reticulate appearance. Antennal segment 3 subtriangular, 4 subtriangular but much larger than 3, 5 subrectangular, 6-10 rectangular, 11 evenly rounded apically (Fig. 105). Pronotum coarsely, evenly, and deeply punctate, punctures recessed producing a reticulate appearance, tubercles and carinae absent; gibbosity evenly rounded, with very faint median longitudinal groove; posterior lobes granulate. Mesoscutellum slightly carinate between posterior lobes of pronotum, posterior



FIGS. 103-105. *Chlamisus texanus*. **103,** dorsal and lateral aspects; **104,** prosternum; **105,** antenna. FIGS. 106-109. *Chlamisus foveolatus*. **106,** dorsal and lateral aspects; **107,** female prosternum; **108,** male prosternum; **109,** antenna. FIGS. 110-112. *Chlamisus quadrilobatus*. **110,** dorsal and lateral aspects; **111,** prosternum; **112,** antenna.

margin slightly depressed and straight except for acute posterolateral angles, sides slightly convergent anteriorly. Metascutellum slightly exposed but undeveloped between anterior elytra. Elytra (Fig. 103) coarsely and deeply punctate, most punctures recessed, producing partially reticulate surface; large, dark spots not reticulate; tubercles lacking or present as small, faint carinae; su-2 small and broad; three small carinae present extending from ae to su-3, from anterior inside margin of umbone to su-2a and from umbone along lateral margin to before apex; anterior elytral suture open, posterior 4/5 serrate. Pygidium evenly, coarsely and deeply punctate, punctures recessed, producing reticulate, slightly convex surface, with small depressions. Prosternum (Fig. 104) twice as long as wide, subtriangular, sides slightly emarginate, center depressed. Metasternum foveolate. First abdominal segment coarsely and deeply punctate, punctures recessed, producing reticulate appearance; last abdominal segment foveolate; mid-ventral fovea broad and deep, surrounded by few short hairs. Well developed tibial spine on front and middle legs.

Aedeagus (Fig. 13) curved, slightly constricted before middle, tubular, with fine apical hairs; apical orifice subterminal, median dorsal plate less than 1/2 width of aedeagus; ejaculatory guide (Fig. 42) tubular, with ventral anterior enlargement; constricted at middle. Female unavailable for dissection.

Types: Female holotype, Brownsville (Cameron Co.), Texas, Charles Schaeffer collection (USNM).

Discussion: Four specimens were available for study. The one from Mexico agrees with the type and the original description. The greenish coloration of the type has faded and the specimen is covered with museum dust, but the identifying characteristics can still be seen. No information is available about food plants.

Specimens examined (3 males and 1 female): (Map 1)
UNITED STATES: TEXAS: Cameron Co., 15 May; Hidalgo Co., 7 Apr.
MEXICO: YUCATAN: Merida, 29-30 July.

Chlamisus foveolatus (Knoch)

Chlamys foveolata Knoch, 1801:130.
Chlamisus foveolata (Knoch); Fattig, 1948:8.

Diagnosis: This species is elongate, black with pale legs, and has a deeply divided pronotal gibbosity, sharp medial carina on pygidium, and a broad prosternal process in females. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male: 2.5-3.0 mm long; 1.4-1.8 mm wide. Female: 2.6-3.3 mm long; 1.5-1.9 mm wide. Color dark brown to black with yellow to light brown appendages; clypeus, lower and middle frons similarly colored; pronotum usually black and elytra dark brown.

Head coarsely punctate, middle frons moderately punctate; medial groove from vertex to middle frons. Antennal segment 3 subcylindrical, 4 subtriangular, 5-10 rectangular, 11 evenly rounded (Fig. 109). Pronotum deeply punctate to foveolate, with obscure foveae laterally; gibbosity with broad punctate groove from anterior margin to posterior lobes; posterolateral slopes nearly perpendicular, posterior lobes tumid and punctate. Mesoscutellum smooth, posterior margin curved and slightly depressed, sides convergent anteriorly; posterolateral angles acute. Elytra (Fig. 106) moderately to coarsely punctate, with sharp tubercles and carinae; most tubercles connected by irregular carinae, ae large and acute; punctures deep, most posterior punctures depressed; straight anterior section of suture short and open, posterior suture serrate. Pygidium moderately to coarsely punctate, with sharp medial carina; apex strongly bent forward, large rounded hump lateral to carina, shallow depressions groove-like from apex to base. Prosternum less than twice as long as wide; prosternal process narrow in male (Fig. 108), wide in female (Fig. 107). First abdominal segment coarsely punctate to foveolate, last abdominal segment coarsely punctate; mid-ventral area with long lateral hairs, flat in male, deeply and broadly foveolate in female. Well developed tibial spine on front and middle legs of male, no tibial spines on female.

Aedeagus (Fig. 14) tubular, strongly curved, without apical hairs; apex with ventral longitudinal keel, slight constriction behind middle; apical orifice round and subterminal, median dorsal plate small and narrow; ejaculatory guide (Fig. 43) tubular, flattened dorsoventrally, with large posterior groove, small dorsal subapical emarginations, apex curved ventrally. Spermatheca (Fig. 71) with long curved cornua, apical 1/2 J-shaped; collum short, tubular, its length equal to basal width of cornua; duct long and coiled; spermathecal gland short and sac-like, about 1/4 as long as cornua.

Type: No type specimen was found in the Berlin Museum where Knoch's types should be located, and none was found elsewhere. The identity of the species is not in question so a neotype is not designated.

Discussion: C. foveolatus has seldom been confused with any other species. The available specimens show a wide distribution in eastern North America and a central Mexican locality. Very little variation is found in specimens from widely separated localities. Several specimens are dark brown rather than black. These are probably teneral or poorly preserved. There is less variation in the sculpturing in this species than in most of the other members of the subfamily in North America.

The species has some resemblance to species of *Exema,* but the genitalia are very different. Detailed examination of sculpturing also reveals the superficiality of this resemblance. There are several South American species

of *Chlamisus* with which *foveolatus* has a very close relationship, even though this is not brought out by Lacordaire's treatment of the species. There are no close relatives in North America.

Plant records: Quercus bicolor (series with larvae), *Rhus toxicodendron.*

Specimens examined (36 males and 74 females): (Map 2)

UNITED STATES: ALABAMA: Mobile Co., 17 June. ARKANSAS: Garland Co., 29 May. DISTRICT OF COLUMBIA: Washington, 4 July. FLORIDA: Bay Co., 20 May; Liberty Co., 15 May. ILLINOIS: state record, no date. INDIANA: Clark Co., 13 June; Marshall Co., 11 June. KANSAS: Riley Co., May; Shawnee Co., 12-25 June. KENTUCKY: state record, no date. LOUISIANA: Natchitoches Par., 28 May. MARYLAND: Baltimore Co., 24 June, 6 July; Montgomery Co., 23 June, 10 July, 24 July, 4 Aug.; Prince Georges Co., 5 Aug. MISSISSIPPI: George Co., 7 May. MISSOURI: Ozark Co., 9 June; St. Louis Co., 24 Aug.-20 Sept. NEW JERSEY: Camden Co., 30 May; Cape May Co., 28 May, 11 June; Gloucester Co., 15 June. NORTH CAROLINA: Harnett Co., no date; Madison Co., no date; Moore Co., 12-18 May, 10 June; Watauga Co., 7 Aug. OHIO: Greene Co., 19 Aug.; Hocking Co., 2 July, 20 July. PENNSYLVANIA: Allegheny Co., no date. SOUTH CAROLINA: state record, no date. TENNESSEE: Montgomery Co., 17 July. TEXAS: Cherokee Co., 3 May; Dallas Co., no date; Gillespie Co., 7 May; Harrison Co., 22 May, 7 June; Leon Co., 18 May; Sabine Co., 27 Mar. VIRGINIA: Nansemond Co., 11 June; Nelson Co., 28 June.

MEXICO: HIDALGO: Jacala, 20 Aug.; 10 mi. NE Jacala, 1-2 Aug.

Chlamisus quadrilobatus (Schaeffer)

Boloschesis quadrilobata Schaeffer, 1926:186-187.
Chlamys quadrilobata (Schaeffer); Leng and Mutchler, 1933:44.
Chlamisus colima Monrós, 1951:257-259 (new synonymy).

Diagnosis: This species is recognized by its small size, black color, highly tuberculate dorsum and completely serrate elytral suture. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male: 2.6-3.3 mm long; 1.7-2.2 mm wide. Female: 2.7-3.5 mm long; 1.9-2.4 mm wide. Color shiny black to brownish bronze; antennae yellowish brown, apical 3-4 segments dark brown; tarsi and inner surface and apex of tibiae yellowish brown.

Head generally moderately punctate, coarsely and deeply punctate above and between antennal sockets, vertex finely and faintly striate; deep depression between eyes below vertex. Antennal segments 3-4 subcylindrical, 5 subtriangular (slightly wider in males than females), 6 subrectangular (Fig. 112). Pronotum finely and deeply punctate, with moderate striae radiating from punctures; gibbosity broadly divided; tubercles well developed, mp and la large and round, anp divided by oblique carina, sm carinate; several other smaller tubercles present; posterolateral slopes deeply punctate, posterior lobes tumid. Mesoscutellum finely striate, posterior margin slightly depressed and curved anteriorly, posterolateral angles acute, sides convergent anteriorly. Elytra (Fig. 110) moderately and deeply punctate, tuberculate and carinate; entire suture serrate; ae large and tuberculate, all other anterior tubercles sharply carinate; posterior tubercles rounded; many posterior punctures with fine radiating striae. Pygidium coarsely

and deeply punctate, with well developed central carina and four central rounded tubercles; basal depression deep. Prosternum (Fig. 111) subtriangular, sides convergent, process less than 1/2 total length. First abdominal segment foveolate with single, rounded tubercle at each side; last segment coarsely punctate, mid-ventral area with few hairs, flat in male, with shallow, broad fovea in female. Large tibial spine on front legs of male only.

Aedeagus (Fig. 15) long and tubular, slightly curved, broadly constricted near middle, apex evenly rounded in dorsal view, pointed in lateral view; lightly sclerotized section over basal foramen less than 1/3 total length of aedeagus; apical orifice subterminal, median dorsal plate narrow; ejaculatory guide (Fig. 44) complex, ventral elongate process attached to two semicircular plates loosely enclosing ejaculatory duct. Spermatheca (Fig. 72) long and slim, cornua elongate, curved, J-shaped, apex slightly narrowed; collum short, length less than width of cornua; spermathecal gland short, sac-like.

Type: San Antonio (Bexar Co.), Texas, Hubbard and Schwarz, USNM type 29466; probably female. The specimen is poorly mounted so that the sex cannot easily be determined. Another specimen, probably a male, same locality, 22 June 1895, H. Sotau, is labeled paratype.

Discussion: Two paratypes of *Chlamisus colima* Monrós from Colima, Mexico, in the United States National Museum, are conspecific with *quadrilobatus*, a species widely distributed in Mexico. On the basis of the paratypes *colima* is synonymized under *quadrilobatus*. Two species closely related to *quadrilobatus* are found in southern Mexico and Central America; further study may reveal others.

The species has no close relatives in North America, but it has a slight resemblance to species of *Exema*. The combination of characters used in the diagnosis and the key may show this species and its relatives are sufficiently distinct to merit being placed in a genus separate from *Chlamisus*. Any such treatment which would divide the North American species of *Chlamisus* would necessitate the naming of at least two or three more new genera.

Plant records: Waltheria americana (series), *Hyptis pectinata, Salvia albida* (series), *Mimosopsis aculeaticarpa, Melampodium divaricatum* and *Sida glutinosa.*

Specimens examined (39 males and 72 females): (Map 1)

UNITED STATES: KANSAS: Douglas Co., 21 Mar. LOUISIANA: Natchitoches Par., 16 Aug. TEXAS: Bastrop Co., 7 Sept.; Bexar Co., Sept.; Kerr Co., 17-23 Apr.; Sabine Co., 27 Mar.; San Patricio Co., 15 Apr.; Uvalde Co., 6 July.

MEXICO: CHIAPAS: 12 mi. N Ocozocoautla, 26 July; 19 mi. W Ocozocoautla, 25 June. COLIMA: Colima, 9 Feb.; 31 mi. E Colima, 19 July. JALISCO: 10 mi. SW Autlán, 22 July; 40 mi. E Guadalajara, 13 June; 11 mi. N Pihuamo, 19 July; Volcán de Colima, no date. MICHOACAN: Morelia, 22 June; 20 mi. N Nueva Italia, 21 June; 7 mi. W Zamora, 15 June. MORELOS: 3 mi. N Alpuyeca, 30 Mar.; Cañon de Lobos, Yautepec, 18 Mar.; Cuernavaca, 17 Mar., May, 4 June, July; 3 mi. N Cuernavaca, 14-21 Mar., 10 Apr.; 5 mi. E Cuernavaca, 29 Mar.; Hueyapán, 8 July; 7 mi. SSW Yautepec, 14 June; "Las Estacas," 6 Apr. NAYARIT:

2 mi. S Acaponeta, 21 Mar.; Jesús María, 7 July; San Blás, 20 June; Tepic, 10 June, 13 Oct. SAN LUIS POTOSI: 20 mi. NE Ciudad del Maíz, 19 June; "6 mi. S Matalpa," 7 July. SINALOA: 32 mi. S Mazatlán, 22 June; 20 mi. N Villa Unión, 19 Aug. SONORA: Alamos, 1 Aug.; "Guirocoba," 6 July. TABASCO: 4 mi. N Teapa, 14 June. TAMAULIPAS: Matamoros, no date. VERACRUZ: Atoyac, 16-17 June; Córdoba, 15 May; Cotaxtla Exp. Sta., Cotaxtla, 23 June; 70 km. W Veracruz, 1 Aug.

GUATEMALA: ALTA VERAPAZ: Trece Aguas, 27 Apr. ESQUINTLA: Finca El Zapote, 7 July; Finca San Victor, 10 Sept.

EL SALVADOR: CUSCATLAN: El Rosario, 24 Mar. SAN SALVADOR: 2.5 mi. W Quezaltepeque, 27 June.

HONDURAS: ATLANTIDA: La Ceiba, 23 Sept.

COSTA RICA: ALAJUELA: Ciruelas, 28 Apr. CARTAGO: Turrialba, no date; 4 mi. E Jicotea, 2 July. GUANACASTE: 3.5 mi. NW Arenal, 28 July; 7 mi. W Arenal, 29 July; 4 mi. NW Cañas, 7-9 July; 7 mi. SE Irma, 31 July; 1-6 mi. SW Los Angeles, 31 July. HEREDIA: Barba, 23 May. PUNTARENAS: Baranca near Puntarenas, 25 Aug.

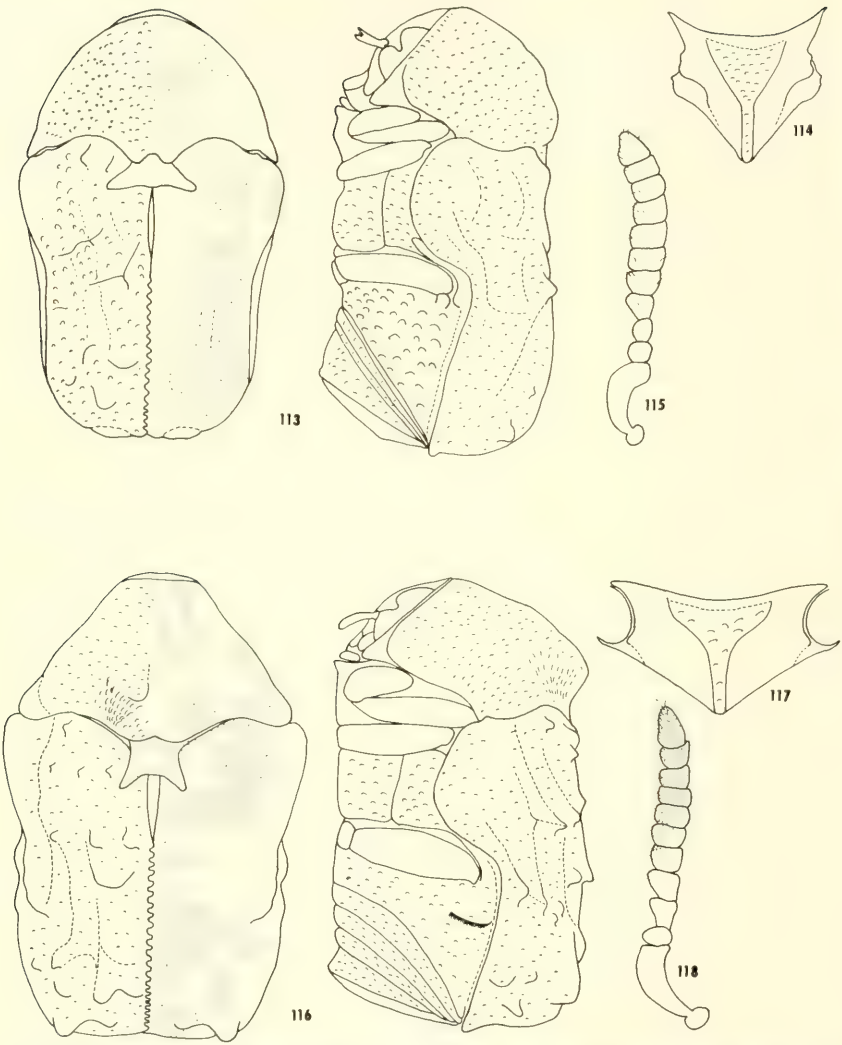
Chlamisus huachucae (Schaeffer)

Chlamys huachucae Schaeffer, 1906:228-229.

Diagnosis: Specimens of *huachucae* are recognized by the unevenly punctate pygidium, dark brown apical 1-2 segments of the antennae, and brown to black color pattern of the elytra and pronotum. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male: 3.1-3.5 mm long; 1.8-2.0 mm wide. Female: 3.5-4.1 mm long; 2.1-2.5 mm wide. Color yellow to reddish brown with irregular markings of light brown to black; antennae yellow with apical 1-2 segments dark brown, posterior margin of pronotum and anterior margins of elytra black; elytral depression and basal 1/3 of pygidium brown; underside except legs generally brown, sides yellow to light brown; margins of prosternum brown.

Head coarsely to finely punctate, vertex coarsely punctate; antennal segment 3 subtriangular, 4-10 rectangular, 11 subconical (Fig. 115). Pronotum coarsely and deeply punctate, punctures depressed causing a reticulate appearance; tubercles absent; gibbosity rounded, faintly divided by broad longitudinal groove, posterior lobes faintly punctate. Mesoscutellum flat; posterior margin emarginate and depressed, sides convergent anteriorly, posterolateral angles acute. Elytra (Fig. 113) coarsely and deeply punctate; tubercles generally carinate, carinae broken and irregular; groups of large, deep punctures in depressions, anterior, posterior and lateral to broad su-2 tubercle; su-3 broad and elongate; complete marginal carina extending from umbone nearly to su-3a. Pygidium coarsely punctate at base to finely punctate at apex, punctures deep; medial carina and depressions faint. Prosternum (Fig. 114) twice as long as wide, with elongate process 1/2 or more of total length, sides gradually convergent posteriorly, more abruptly convergent in females. First abdominal segment coarsely punctate, punctures depressed, producing reticulate appearance; last abdominal segment moderately punctate, mid-ventral area flat with long lateral and anterior



FIGS. **113-115.** *Chlamisus huachucae*. **113,** dorsal and lateral aspects; **114,** prosternum; **115,** antenna. FIGS. **116-118.** *Chlamisus nigromaculatus*. **116,** dorsal and lateral aspects; **117,** prosternum; **118,** antenna.

hairs in male, deeply foveolate with long lateral hairs in female. Large tibial spine on front and middle legs of male, no tibial spines on female.

Aedeagus (Fig. 16) curved, tubular, strongly bent at middle and gradually flattened toward apex; apex bluntly pointed in dorsal view; ejaculatory guide (Fig. 45) tubular, slightly narrowed behind, with anterior medial process. Spermatheca (Fig. 73) simple, J-shaped; collum thin, tubular, longer than width of cornua.

Types: A male syntype (USNM no. 42-603) is here designated the lectotype. The specimen is labeled as follows: Palmerlee, Cochise Co., Arizona, 9 July, Brooklyn Museum Coll. 1929. There are also three female syntypes (USNM no. 42305) with the same locality data, collected on 14 June and 9 July.

Discussion: C. huachucae is one of the pale southwestern species. It can easily be separated from the other species, especially *arizonensis* with which it is most easily confused, by the diagnostic characters.

This species is similar to *Exema* and *Neochlamisus* in the structure of the aedeagus and spermatheca. It has coloring and sculpturing similar to those of the pale species of *Chlamisus* and *Pseudochlamys*. The shape of the aedeagus and spermatheca and similar antennal and elytral punctations indicate a close relationship of *huachucae* to *nigromaculatus* n. sp.

The small number of specimens studied show little variation except in the degree of darkness of the color pattern and the usual variation in punctures and tubercles. No information on host plants is available.

Specimens examined (6 males and 21 females): (Map 2)

UNITED STATES: ARIZONA: Cochise Co., 14 June, 2-29 July; Pima Co., 10-20 June, 11 Aug.; Santa Cruz Co., 9 June, 20 June, 4-20 July, 3-4 Aug., 23 Aug.

MEXICO: COAHUILA: nr. Jame, 33 mi. SE Saltillo, 18 July. SONORA: Yecora, 20-22 May.

Chlamisus nigromaculatus new species

Diagnosis: The extensive dark markings on the pronotum and elytra, unevenly rounded pronotal gibbosity with striopunctate posterolateral slopes, and wide black markings on the upper frons are distinctive. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male holotype: 3.5 mm long; 2.1 mm wide. Color yellow to light brown with extensive black markings covering most nontuberculate areas; ventral surface black with lateral yellow spots; legs light brown with dark central areas on tibiae and femora; head with wide black inverted V extending from antennal sockets to vertex, narrow transverse black band across vertex and along dorsal margin of eye to inverted V; pronotum irregularly marked with large black spots, posterolateral slopes black; posterior margin of pronotum and anterior margins of elytra black. Mesoscutellum yellow with continuous black margins. Elytral tubercles, lateral and sutural margins and apex yellow. Pygidium with several irregular basal black spots, many black central and lateral punctures.

Head coarsely punctate, clypeus and lower frons moderately punctate; antennal segment 3 subtriangular, 4 subrectangular, 5-10 rectangular, 11 subconical (Fig. 118). Pronotum coarsely and deeply punctate, tubercles absent; gibbosity faintly divided posteriorly, its summit rough with irregular depressed punctures; posterolateral slopes striopunctate, posterior lobes poorly developed and punctate. Mesoscutellum flat, subquadrate, with

projecting posterolateral angles. Elytra (Fig. 116) coarsely punctate, with well developed tubercles and carinae; su-2 broad, su-3 broad and elongate, anterior tubercles rounded or acute; anterior elytral suture open, but metascutellum not visible, posterior 3/4 of suture serrate. Pygidium coarsely punctate basally to finely punctate at apex; depressions and medial carina faintly developed or absent. Prosternum (Fig. 117) subtriangular, slightly longer than wide. First abdominal segment coarsely punctate (large transverse groove on left side only in this specimen); last abdominal segment coarsely punctate; mid-ventral fovea shallow on posterior half of segment, with long anterior and lateral hairs; numerous long hairs on mid-ventral posterior margin of first four abdominal segments.

Aedeagus (Fig. 17) curved, tubular, flattened dorsoventrally toward apex, with subapical hairs on ventral surface; apical orifice subcentral, median dorsal plate wide; apex evenly rounded in dorsal view; ejaculatory guide (Fig. 46) long and complex, with anterior ventral keel, posterior dorsal margins broadly separated.

Female allotype: 3.7 mm long; 2.2 mm wide. Color and sculpturing as in male; prosternal process narrower than in male; numerous short hairs on mid-ventral posterior margin of first four abdominal segments: mid-ventral fovea of last abdominal segment large and deep; no tibial spines. Spermatheca (Fig. 74) with cornua nearly U-shaped; collum short and subtriangular, length equal to width of cornua; spermathecal duct long and convoluted.

Types: Male holotype: Chiricahua Mts. (Cochise Co), Arizona, 22 July 1953, D. J. and J. N. Knull (OSU). Same data on 1 ♀ paratype (JAW). Female allotype with same data except collected on 20 July 1953 (OSU). (Map 1.)

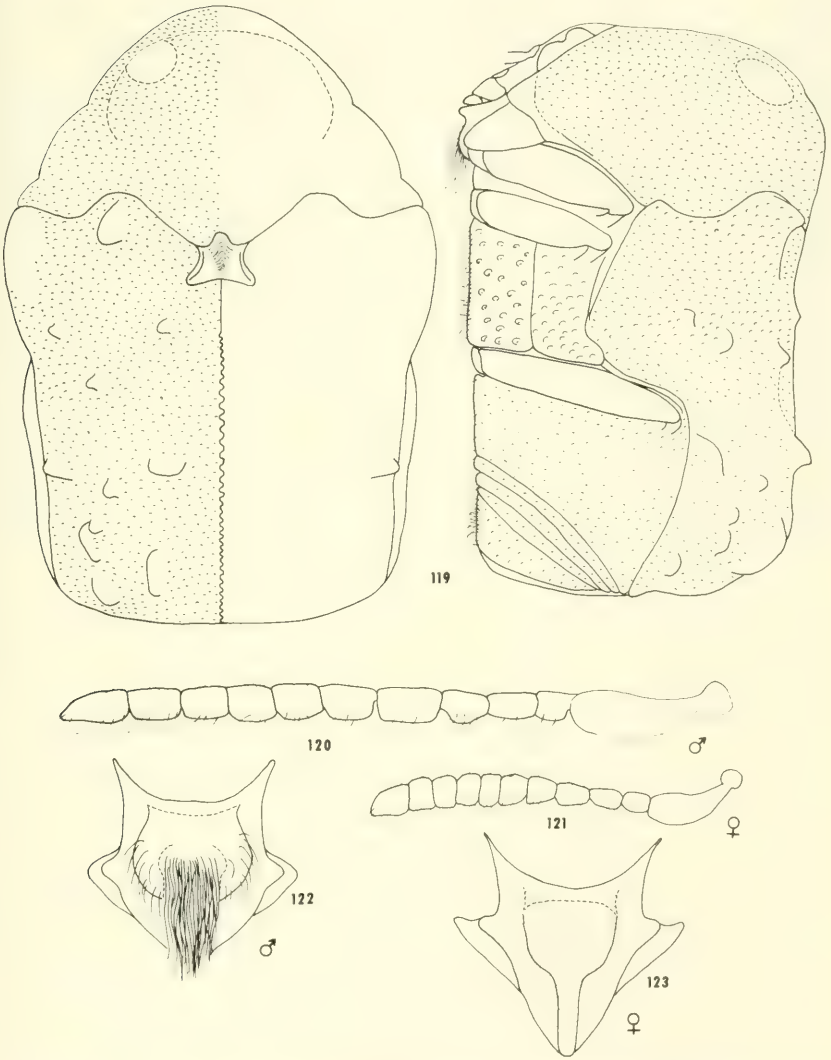
Discussion: Only the short type series was available for study. The name is chosen to describe the numerous black markings on the dorsum of the beetle. The species is more closely related to *huachucae* than to other members of the genus but differs in the characters mentioned in the diagnosis. It likewise has some similarities to species of *Exema* and *Neochlamisus* in the form of the aedeagus and spermatheca. No host plants are known.

Chlamisus maculipes (Chevrolat)

Chlamys maculipes Chevrolat, 1835:120.
Chlamisus maculipes (Chevrolat); Blackwelder, 1946:649.

Diagnosis: This is the only highly pubescent North American *Chlamisus*. In addition it is characterized by its large size and yellow ventral and black dorsal surfaces. The males have elongate antennae and long decumbent hairs on the prosternum and metasternum. The aedeagus, ejaculatory guide and spermatheca are also diagnostic.

Description: Male: 3.6-6.0 mm long; 2.5-3.9 mm wide. Female: 4.4-6.0



Figs. **119-123.** *Chlamisus maculipes.* **119,** dorsal and lateral aspects; **120,** male antenna; **121,** female antenna; **122,** male prosternum; **123,** female prosternum.

mm long; 3.0-4.1 mm wide. Color of dorsum black, venter yellow with black markings, lateral and anterior margins of pronotum yellow; head yellow, with light brown to black spot on vertex; legs yellow with light brown to black central spot, tarsi yellow, claws black; prosternum black, coxal articulation black, pygidium black with lateral and apical margins yellow; abdomen black with yellow border.

Head finely and faintly punctate, curved hairs on upper frons near eyes; antennae in male (Fig. 120) extend beyond posterior margin of prosternal process, segment 3 subconical, 4 subtriangular, 5-10 rectangular, but length greater than width; antennae of female (Fig. 121) short, not reaching posterior margin of prosternal process, segment 3 subcylindrical, 4 subtriangular, 5 subrectangular, but longer than wide, 6-10 subquadrate; segment 11 in both sexes elongate, bluntly pointed. Pronotum nontuberculate, coarsely punctate, punctures obscured by 3-5 curved hairs from each puncture, two nonpubescent areas on upper anterior slope of gibbosity, gibbosity feebly divided, posterior lobe punctate. Mesoscutellum carinate between posterior lobes of pronotum, lateral margins finely striate, carinate and slightly convergent, posterior margin curved and depressed, posterolateral angles acute. Punctation and pubescence of elytra (Fig. 119) similar to pronotum except scattered tubercles smooth; ae, su-1a, su-2, su-2a, ma-b and su-3a usually present and well developed, ma faintly carinate; elytral suture serrate except for short distance behind mesoscutellum. Pygidium punctate and pubescent, resembling elytra, depressions obscure or lacking; medial carina faint, smooth. Prosternum tumid, with numerous long hairs in male (Fig. 122), short curved hairs in female (Fig. 123). Punctures and pubescence of venter similar to those of dorsum, lateral punctures of thorax foveolate and widely separated; large central area of metasternum of male with numerous long straight hairs; central punctures of last abdominal segment, each with a single hair. Mid-ventral area of last abdominal segment in male flat with short lateral hairs, mid-ventral fovea of female large and shallow with long lateral hairs. Well developed tibial spine on front and middle legs of male; no tibial spines on female.

Aedeagus (Fig. 18) long, curved, tubular, flattened dorsoventrally toward apex; apex explanate, with posterolateral triangular process; apical orifice subcentral, median dorsal plate narrow and forked; large lateral and small ventral subapical hairs; ejaculatory guide (Fig. 47) long, tubular, with dorsal and ventral anterior processes; posterior, long, curved, explanate plates open. Spermatheca (Fig. 75) widely J-shaped; collum shorter than width of cornua; duct long and convoluted.

Type: The type cannot be found or recognized in material from the British Museum where it should be located. The original description is brief, but since the species is easily characterized there is no doubt about its identity.

Discussion: The many unique characters found in this species suggest that it should have generic status, together with several related Mexican species. The present name of the species should remain unchanged until there is a better understanding of its relationships with other species and species groups.

The species is placed in *Chlamisus* but nearer *Diplacaspis* and *Neochlamisus* because of the similarities in the aedeagus, ejaculatory guide and spermatheca. Although in some ways specialized, these structures in *maculipes* could represent intermediate steps in the evolution of their more highly specialized counterparts in the latter genera.

There is considerable variation in the ventral color pattern of *maculipes*. For example, the last abdominal segment may range from completely yellow to completely black. The central black spot on the pygidium varies from small to large, leaving only a narrow yellow margin. Females are generally darker than males because of larger black markings. I cannot correlate any color variation with geographic distribution.

Size variation is probably greater in this species than in any other in North America. The specimens from Texas are among the smallest members of the species.

Finally, the variation in the size of elytral tubercles is especially noticeable. It is not any greater than that found in other North American species, but it is more obvious because of the large size of most specimens and the small number of tubercles on the elytra.

Specimens have been collected over a wide range in Mexico and Central America, as well as in southernmost Texas. Individual beetles have been collected on a number of unidentified plants. One, together with larvae, was collected on *Ipomaea pedicellaris,* and one female was observed ovipositing on *Verbesina fraseri.* The species probably feeds on a variety of plants.

Specimens examined (52 males and 76 females): (Map 2)

UNITED STATES: TEXAS: Cameron Co., 25 May-9 June, 12 July.

MEXICO: CAMPECHE: 10 mi. N Hopelchén, 17 Apr. CHIAPAS: 4 mi. NE Pichucalco, 14 June; 1 mi. SW Simojovel, 19 Mar. COLIMA: Colima, no date. GUERRERO: Acapulco, 10 Aug.; Iguala, 2 June; 8 mi. N Iguala, 23 Aug.; Taxco, 2 Aug. JALISCO: Volcán de Colima, 6 June. MORELOS: Cuernavaca, July; 7 mi. SSW Yautepec, 14 June, 2 July, 28 July. NAYARIT: Jesús María, 26 June; Tepic, 10 June, 20-24 July; 10 mi. NW Tepic, 1 Sept. OAXACA: Almoloya, no date; 44 mi. N Matías Romero, 19 June; Rincón Antonio, no date; Tehuantepec, 29 June. PUEBLA: Acatlán, 17 June; Huauchinango, no date. SAN LUIS POTOSÍ: Ciudad de Valles, July, 29 Aug.; Salto del Agua, 28-30 June; Tamazunchale, 19 June. TABASCO: Teapa, no date. VERACRUZ: Atoyac, 16-17 June; Córdoba, 8 May, 10-14 June; Cotaxtla Exp. Sta., Cotaxtla, 27 June, 12 July; 2 mi. N El Cedro, 7 June; Fortín, 8 July; Jicaltepec, 14-20 Mar.;10 mi. NE Minatitlán, 4 July; Orizaba, June; Playa Vicente, no date; Puente National, 21 June, 3 July; Rinconada, 29 June; San Andrés Tuxtla, no date; Veracruz, no date; 20 mi. S Veracruz, 16 June. "Yucatán," no date.

GUATEMALA: ALTA VERAPAZ: Panzos, no date. RETALHULEU: Champerico, Aug.

BRITISH HONDURAS: "M-Tee Dist.," 12 June.

HONDURAS: MORAZAN: Zamorano, July.

NICARAGUA: no locality, no date.

COSTA RICA: GUANACASTE: 4 mi. NW Tilarán, 30 July. SAN JOSE: Santa Ana (?), 12 Apr.; San José, no date. "Borroeta," 4-8 Apr.

Diplacaspis Jacobson, 1924

Diaspis Lacordaire, 1848:645-646.
Diaspsis Lacordaire; Jacoby, 1889:155 (misspelling).
Diplacaspis Jacobson, 1924:239 (new name for *Diaspis* Lac., not Costa, 1835, Coccidae).
Skwarraia van Emden, 1932:9 (new name for *Diaspis* Lac.).

Type species: Diaspis paradoxa Lacordaire (monotypic).

History: The genus *Diaspis* was established by Lacordaire for a unique Mexican species having a visible second scutellum and bifid tarsal claws. A second species was described by Baly (1878) from the Amazon region of Brazil. Jacoby (1881) added two more Mexican species to the genus by transferring *moestificus* and *memnonius* from *Chlamys* since they have an exposed second scutellum. He also expressed some doubt about the validity of this structure as a generic character. The name *Diaspis* proved to be a junior homonym of *Diaspis* Costa (1835), an important genus of Homoptera. Jacobson (1924), proposed the replacement name *Diplacaspis,* now the valid name. Unaware of Jacobson's publication, van Emden (1932) proposed the new name *Skwarraia* for the genus. Navajas (1944b, 1946) pointed out this synonymy in his review of the nomenclature and type species of the Chlamisinae.

Monrós (1954), after studying the type material in the United States National Museum, transferred the North American species, *prosternalis, scabripennis* and *subelata* from *Chlamys* and *Boloschesis* to *Diplacaspis.* The Mexican species *pici* was described by Monrós (1959) and as a result of the synonymizing of *pici* with *prosternalis* and removal of *moestifica, memnonia, scabripennis* and *subelata* from *Diplacaspis,* the genus now contains nine species.

Diagnosis: The genus is characterized by having bifid claws, and expanded prosternal process between the mesocoxae, a flattened, curved aedeagus, and an elongate, pointed, symmetrical ejaculatory guide with a small or partial sheath.

Description: Male: 2.7-4.5 mm long; 2.2-3.2 mm wide. Female 2.7-3.5 mm long; 2.0-2.7 mm wide. Color shiny black to reddish or greenish bronze; antennae yellowish brown.

Head finely to coarsely punctate, vertex sometimes striopunctate, upper frons with slight central depression. Antennal segment 1 shorter than normal for the subfamily, 2 subcylindrical and shorter than 3, 3-4 subcylindrical and subequal, 5 subtriangular, 6-10 rectangular, 11 subconical. Pronotum finely and deeply to moderately and faintly punctate, sometimes moderately and irregularly striate; gibbosity evenly rounded to highly tuberculate, faintly to deeply divided; posterior lobes smooth to faintly punctate; tubercles well developed or absent. Mesoscutellum subquadrate, sides faintly to strongly convergent anteriorly, posterior margin straight and slightly depressed, posterolateral angles slightly reflexed. Metascutellum

projecting between anterior 1/3 of elytra, rounded or sharply carinate, broadly exposed. Elytra finely to moderately punctate, punctures deep or depressed; tubercles faint to large and sharply carinate, granulate or finely striate; anterior 1/3 of elytral suture broadly opened, exposing metascutellum, posterior 2/3 serrate. Pygidium slightly convex and tuberculate, with central carina or faint longitudinal groove, moderately to coarsely punctate; deep punctures near apex and in lateral depressions. Prosternum coarsely punctate with lateral margins convergent anteriorly, process expanded between mesocoxae, its apex bluntly pointed; central area slightly depressed. First abdominal segment punctate to obscurely foveolate laterally, with two lateral depressions; last segment punctate or foveolate, midventral area in male flat or longitudinally grooved, with numerous recurved hairs, in female with large, deep fovea, lateral hairs short and scattered. Single tibial spine on front and middle legs of both sexes, smaller in female than in male. Tarsal claws bifid.

Aedeagus long and curved, gradually flattened dorsoventrally toward apex; apex truncate to long-pointed, apical orifice subcentral; ejaculatory guide symmetrical, with small to large sheath, anterior half with dorsal, paired, long, pointed plates. Spermatheca J-shaped, apex of cornua gradually narrowed, duct long and convoluted.

Distribution: The species are most numerous in Brazil but one occurs in the Southern United States, and several occur in southern Mexico and Central America.

Systematic position: In sculpturing and form of the pronotum and elytra, *Diplacaspis paradoxa* from Mexico resembles species of *Mellitochlamys*. Other characters, however, indicate no close relationship between the genera. The shape of the prosternum could be a modification of that found in any of the related genera.

Most of the species of *Diplacaspis* resemble *Neochlamisus* more closely than any other chlamisine genus. Each genus has several specialized characters shared with some or all of the species of the other. A combination of characters is necessary to distinguish all of the species.

The faintly striate pronotum and elytra resemble those commonly found in *Neochlamisus* and a few species of *Chlamisus*. The form of the spermatheca is similar in all three genera. The form of the ejaculatory guide suggests a close relationship to *Neochlamisus*. The flattened aedeagus is similar to those of the above genera, but several others have the same form for this structure. The highly tuberculate sculpturing, large, deeply divided pronotal gibbosity and foveolate abdomen are characters found in all three genera. In spite of the close relationships mentioned above, there is sufficient discontinuity for generic distinction in *Diplacaspis*. It has an

intermediate position between *Neochlamisus* and the more specialized species of *Chlamisus*.

Discussion: The diagnosis and description above are compiled from information about the North American and Mexican species of *Diplacaspis* that I have studied. Published descriptions of several South American species indicate the tarsal claws are not always bifid and the prosternal process is not always expanded between the coxae. Nevertheless, the use of these characters aids in the identification of the North American and Mexican species.

With the transfer of four species to the new genus *Neochlamisus,* the remaining nine are a more closely related group. Although the exposed second scutellum is present in all of them, the character is not diagnostic because it is found in other genera. However, chlamisines possessing this character and lacking deep, closely set punctures which give the appearance of velvety spots are all in *Diplacaspis*.

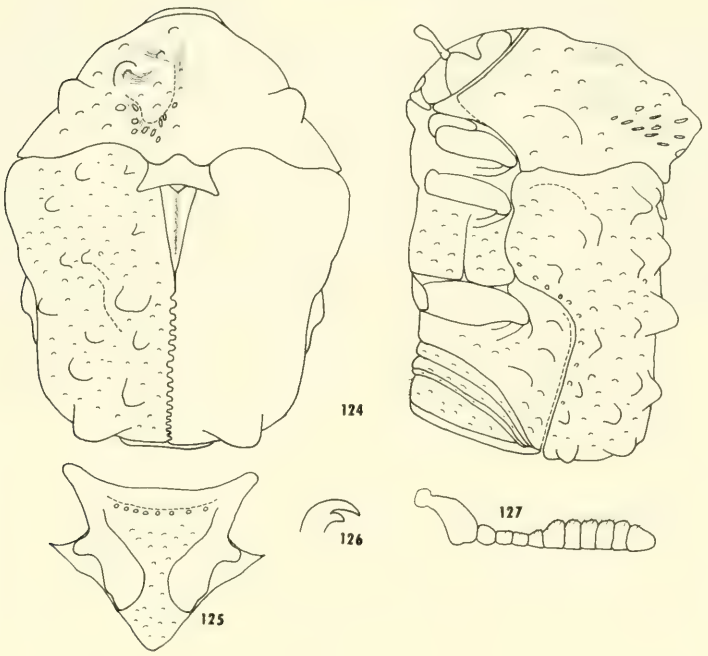
Drawings of the male genitalia of the Mexican *D. paradoxa* (Figs. 20, 48) have been included for comparison with *prosternalis* and species of *Neochlamisus*. Reliable plant records for two different species suggest *Diplacaspis* has a preference for *Acacia* spp. Only one species, with a wide distribution in Mexico, is found in the United States.

Diplacaspis prosternalis (Schaeffer)

Chlamys prosternalis Schaeffer, 1906:227.
Boloschesis prosternalis (Schaeffer); Schaeffer, 1926:186.
Chlamisus prosternalis (Schaeffer); Blackwelder, 1946:649.
Diaclaspis (sic) *pici* Monrós, 1959:3-4 (new synonymy).

Diagnosis: The species is easily recognized by the bifid claws and expanded prosternal process. The absence of velvety spots on the elytra when the metascutellum is broadly exposed distinguishes *prosternalis* from the *velutinus* species group in *Neochlamisus*. The genitalia are also diagnostic for this species.

Description: Male: 2.7-3.4 mm long; 2.2-2.7 mm wide. Female: 2.7-3.5 mm long; 2.0-2.7 mm wide. Color shiny black to reddish bronze; antennae light brown. Head coarsely punctate, vertex striopunctate, clypeus and lower frons moderately punctate, upper frons with slight central depression. Antennal segments 3-4 subcylindrical, 5 subtriangular, 6-10 rectangular (Fig. 127). Pronotum finely and deeply punctate, moderately, irregularly striate except laterally; tubercles well developed, su, la and mp large and rounded; gibbosity deeply divided; posterolateral slopes with 5-7 large deep punctures; posterior lobes smooth, tumid. Mesoscutellum subquadrate, sides slightly convergent anteriorly, posterior margin straight, slightly depressed, posterolateral angles slightly reflexed. Metascutellum well developed, sharply carinate, broadly exposed. Elytra (Fig. 124) moderately and deeply



Figs. **124-127.** *Diplacaspis prosternalis*. **124,** dorsal and lateral aspects, **125,** prosternum; **126,** tarsal claw; **127,** antenna.

punctate, with well developed, broad tubercles usually not carinate; tubercles finely striate, faintly punctate; anterior 1/3 of elytral suture broadly open, exposing metascutellum, posterior 2/3 serrate. Pygidium convex, coarsely punctate near apex and in four lateral and two deep basal depressions; faint medial carina with deep lateral punctures. Prosternum (Fig. 125) narrowed between procoxae then expanded between mesocoxae, apex rounded, central area slightly depressed. First abdominal segment punctate to obscurely foveolate laterally, with two lateral depressions; last segment foveolate, mid-ventral area with numerous recurved hairs in male, female with large deep fovea, lateral hairs short and scattered. Tibial spine on front and middle legs of both sexes, spines smaller in female than in male. Tarsal claws (Fig. 126) bifid.

Aedeagus (Fig. 19) curved and tubular, gradually flattened dorsoventrally toward apex; apex narrowly truncate; ejaculatory guide (Fig. 49) symmetrical, with two long, dorsal acute processes and a partial sheath. Spermatheca (Fig. 76) J-shaped, cornua gradually narrowed toward apex; collum short and narrow, shorter than width of cornua; duct long and convoluted.

Types: A male in the U.S. National Museum, with the following label data, is here designated the lectotype: Brownsville (Cameron Co.), Texas; Brooklyn Museum Coll. 1929; cotype no. 42304 USNM. There are three syntypes from the Brownsville area with the following data: Esperanza Ranch, July; Yucca Ridges, 6 Aug. (USNM).

Discussion: The species was first described in the genus *Chlamys*. Because of the broadly exposed second scutellum it was transferred to *Diplacaspis*. A comparison of *prosternalis* with *paradoxa* shows a considerable difference in the sculpturing and shape. The tubercles, carinae and the gibbosity are larger in *prosternalis* than in *paradoxa*. The shape (dorsal outline) of *prosternalis* is subquadrate compared to the almost oval shape of *paradoxa*. Intermediate forms are represented in the South American species. The two species are considered congeneric on the basis of similarities in claws, prosternum, genitalia and metascutellum.

The description of *pici* was taken from a manuscript of Monrós. There was no mention in his publication of *prosternalis*, a species that must have been unknown to him. On the basis of the original description of *pici* and specimens from the type locality, I consider it conspecific with *prosternalis*.

Plant records: Acacia farnesiana, A. greggii, Gaillardia sp. and *Suaeda*? sp.

Specimens examined (41 males and 62 females): (Map 3)

UNITED STATES: ARIZONA: Pima Co., 4 Apr., 15 May-8 June, 23 June-30 July, 10-13 Aug. TEXAS: Cameron Co., 4-13 Apr., 25 May, 20 June, 8 Aug.; Kinney Co., 27 Aug.; Live Oak Co., 25 Mar.; Starr Co., 28 Mar., 9 Apr.; Uvalde Co., 6 July.

MEXICO: BAJA CALIFORNIA SUR: 10 mi. SW San José del Cabo, 9 July; Triunfo, 7 July. CHIAPAS: 28 mi. W Cintalapa, 9 Apr. GUERRERO: Acapulco, Oct. NAYARIT: 70 mi. S Acaponeta, 22 Aug. NUEVO LEON: Monterrey, 1 Jan.; 5 mi. S Monterrey, 6 July, 25 Feb. OAXACA: Oaxaca, no date; 10 mi. NE Oaxaca, 20 June. PUEBLA: 30 mi. NW Petlalcingo, 3 Apr. SINALOA: 30 mi. E Villa Unión, 7 July. SONORA: Guaymas, 10 Apr.; San Pedro Bay, 7 July. TAMAULIPAS: Tampico, 26 Mar. VERACRUZ: St. Lucrecia, no date; Tuxpan, 18 Aug.; Veracruz, no date.

GUATEMALA: ALTA VERAPAZ: Lanquin, 5-8 June.

NICARAGUA: GRANADA: Granada, no date.

Neochlamisus new genus

Type species: Neochlamisus velutinus new species (present designation).

This genus includes 16 North American species formerly in *Diplacaspis* and *Chlamisus*, several of which extend their distribution into Mexico, plus several Central American species. A few South American species also appear to have similar characteristics.

Most if not all of the references to North American species of *Chlamisus* also refer to species of *Neochlamisus* and will not be repeated here. Specific references will be found under the species headings.

Diagnosis: The ejaculatory guide of the aedeagus is asymmetrical and partially enclosed in a sheath. The spermatheca is J-shaped or U-shaped

and enlarged near the apex of the cornua. The spermathecal duct is long and convoluted. In addition North American species can be identified by the presence of either velvety spots on the elytra or striations on the posterolateral slopes of the pronotum.

Description: Male: 2.8-4.8 mm long; 2.1-3.7 mm wide. Female: 2.9-4.9 mm long; 2.2-3.8 mm wide. Color dark brown to bright bronze, generally with yellow, blue, green, or red metallic reflections; frons in emargination of eye with or without yellow spot; underside, legs and tarsi similar in color to dorsum; antennae yellow to light brown; labrum light reddish brown; mandible and palpi dark reddish brown.

Cuticle minutely granulate. Head with slightly to deeply depressed medial area on front, finely to coarsely punctate, sometimes striate or vermiculate. Antennal scape and pedicel normal for the subfamily, segment 3 longer than wide, subcylindrical, segments 4-10 compressed, bluntly serrate, subtriangular to rectangular in outline, segments finely pubescent and with 6-8 long hairs, segment 11 subconical, slightly flattened. Pronotum faintly to moderately tuberculate, nonstriate to coarsely and regularly to highly irregularly striate, finely to moderately punctate; posterolateral slopes striopunctate or striate, irregular striae converging on area near middle of lateral margin, anterior slope always more finely and irregularly striate; gibbosity slightly to deeply divided, posterior lobes smooth to striate, sometimes with scattered punctations. Mesoscutellum subquadrate, impunctate, granulate or finely to moderately striate. Metascutellum covered by elytra or exposed, smooth, shiny, carinate, and highly developed between anterior 1/5 of elytra when exposed. Anterior margin of each elytron crenate from scutellum to past middle of humeral umbone except short area anterolateral to tubercle ae; elytra granulate, sparsely to confluently punctate or rugose, highly tuberculate and carinate; anterior tubercle acute to blunt, posterior tubercles usually evenly rounded; suture serrate on posterior 4/5 only; some species with two velvety spots on disc lateral to and anterior to tubercle su-2, usually separated by oblique carinae from tubercle su-2 to umbone; tubercles, carinae and deep puncture finely striate. Pygidium granulate, medial carina usually complete; foveae shallow to deep, faintly to deeply punctate, mostly confluent and highly granulate, lateral areas usually more coarsely punctate; posterolateral, elongate depressions small to moderate, apical area moderately punctate. Prosternum goblet-shaped, coarsely punctate, center of anterior half flat to slightly impressed; posterior process narrow or explanate, with lateral serrations. Anterior edge of metasternum between mesocoxae with two blunt processes between which prosternal process fits; ventral surface appearing reticulate, with punctures in shallow to deep, close or sometimes confluent foveae. First abdominal segment with lateral process partly covering apex of femur and base of

tibia, in repose; many circular confluent foveae producing large shallow depressions dorsal and posterior to process; Y-shaped carina between coxae accentuated by punctures; regular row of small foveae on posterior border of each abdominal segment; last abdominal segment with large, shallow to deep fovea on mid-ventral area in female, always less impressed in male, surrounded in both by short posterior and anterior hairs, lateral hairs longer, anterior hairs sometimes lacking in female. One or two tibial spines usually well developed, generally curved inward, on front leg of male, present or absent in female; middle legs with or without tibial spines, which may be obscured by the apical spurs and setae.

Aedeagus explanate and truncate to round or pointed; apical orifice subcentral, short longitudinal row of lateral hairs before apex; ejaculatory guide asymmetrical, short to long; spermatheca J-shaped or U-shaped, apex of cornua slightly enlarged; collum short, sometimes slightly enlarged, shorter than width of cornua; duct long and highly convoluted.

Systematic position: *Neochlamisus* is placed at the end of this revision because of its many specialized characters, including asymmetrical ejaculatory guide, ejaculatory sheath, variation in tibial spines, pronotal striation, yellow spot on the frons in the emargination of the eye (except *velutinus* and *memnonius*) and in some species the exposed metascutellum and velvety spots on the elytra. A close relationship to *Diplacaspis* is suggested by the occurrence of several of these characters in both genera, as discussed under that genus. Many of these similarities involve only a few species of each genus. The structural similarity in the aedeagus, pronotal striation and the tubercles of the elytra suggests some relationship of *Neochlamisus* to North American *Exema*, but the resemblance is not as strong as to *Diplacaspis*. The character states of *Neochlamisus* are probably more recent specializations than the corresponding ones found in the other two genera.

Discussion: Two distinct species groups can be recognized in the genus: the species formerly included in *Diplacaspis* and those formerly in *Chlamisus*. I have named these only as species groups since it seems that subgeneric status would contribute nothing to an understanding of them.

On the basis of the interspecific similarity in both male and female genital structures, the species of this genus are more closely related than are those within any of the other genera studied. The ejaculatory guides of the North American species are all of the same general shape. This structure in *velutinus* and *memnonius* has some similarity to those of the *gibbosus* species group and suggests the relationship of the two groups. Specific variation is more apparent in the sculpturing of various parts of the body.

Key to Species Groups of *Neochlamisus*

1a. Two velvety spots on each elytron divided by oblique carina; pronotum faintly striate or striopunctate; metascutellum exposed between elytra (except in *moestificus*); tip of aedeagus explanate to truncate; spermatheca J-shaped with slightly enlarged apex; anterior and middle tibiae with one apical spine in both sexes ..... *velutinus*

b. No velvety spots or only faint traces of them on each elytron; pronotum faintly to coarsely striate; metascutellum seldom and only slightly exposed; tip of aedeagus truncate to acute; spermatheca J-shaped with noticeable knob on apex; anterior tibiae of males with two apical spines (except only one in *chamaedaphnes* and *fragariae*), middle tibiae with one spine, females usually with one spine (very small in some) on anterior tibiae ..... *gibbosus*

velutinus Group

The following species, formerly included in the genus *Diplacaspis,* are included in the *velutinus* species group: *memnonius, moestificus, scabripennis, velutinus* n. sp., and *subelatus.* Examination of the male and female genitalia indicates that *Diplacaspis paradoxa* is not congeneric with the above species, which are closely related to the North American species of the *gibbosus* group. The supposition that the *velutinus* and *gibbosus* groups are congeneric is supported by similarity in sculpturing, punctation, size, and coloring, as well as in both male and female genitalic structures.

Most authors have doubted the validity of the genus *Diplacaspis* since all species with an exposed second scutellum were included without regard to other characters in which they differed from the type species. Considerable inter- and intraspecific variation of this character reduces its value as a generic indicator, but it does indicate a relationship between the two species groups and a certain degree of affinity among species. The presence of a second scutellum remains a generic character in *Diplacaspis* but differentiation of the genus in North and Central America is also based upon the shape of the prosternum, bifid claws, shape of the aedeagus and the development of the ejaculatory guide.

The relationship between the *velutinus* and *gibbosus* species groups is also suggested by two other characters, velvety spots on the elytra and the presence of apical spines on the front and middle tibiae. One species of the *gibbosus* group has a small velvety spot in the discal area, some specimens of two other species have faint indications of velvety spots, and two other species have the single tibial spine characteristic of the *velutinus* species group.

The species of this group are most easily identified by the presence of the visible second scutellum and the velvety spots on the elytra. One Mexican species, *memnonius* is included here because of its similarity to

velutinus n. sp. The two have been known under the same name for many years.

KEY TO THE *velutinus* SPECIES GROUP

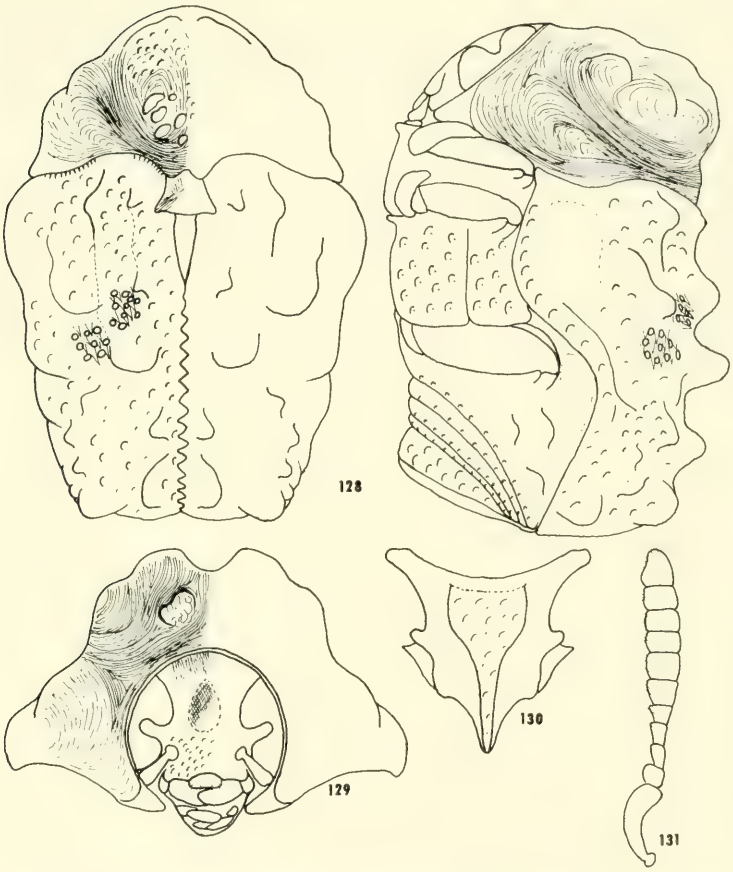
1a. Emargination of eye without a yellow spot 2
b. Emargination of eye with a yellow spot 3
2a. Velvety spots large and confluent, each including more than 20 deep punctures; oblique carinae obscured by large velvety spots ..... *memnonius*
b. Velvety spots small, each including about 10 deep punctures, separated by a high, sharp, oblique carina ..... *velutinus* n. sp.
3a. Pronotal gibbosity shallowly divided; color coppery; elytral sculpture coarsely punctate-rugose; areas between punctures carinate ..... *subelatus*
b. Pronotal gibbosity moderately to deeply divided; color coppery to metallic black; elytral sculpture coarsely to moderately punctate; areas between punctures granulate 4
4a. Metascutellum broadly exposed and projecting between elytra, exposed anterior margin ¼ as wide as mesoscutellum; posterior lobes of pronotum distinctly striate; mesoscutellum faintly striate to rugose; elytra shiny granulate, slightly rugose, punctures large and confluent, color bright reddish bronze; scutellar tubercle small ..... *scabripennis*
b. Metascutellum narrowly to scarcely exposed; posterior lobes of pronotum faintly striate; mesoscutellum smooth granulate, often with a carina or tubercle in posterior part of pronotal groove; elytra sparsely to moderately punctate, punctures usually distinct and separated; color bright coppery to dark bronze; scutellar tubercle faint to carinate; pronotum striopunctate ..... *moestificus*

Neochlamisus velutinus new species

Diagnosis: The absence of a yellow spot on the frons in the emargination of each eye, the high and deeply divided pronotal gibbosity, large, high, carinate elytral tubercles, subtrunctate aedeagus, and long, slender ejaculatory guide together serve to distinguish this species from all others in the genus.

Description: Male holotype: 3.8 mm long; 2.9 mm wide. Color dark brownish bronze with small areas of metallic blue, purple, and red reflections. Antennae yellowish brown; labrum light reddish brown; mandibles and palpi dark reddish brown; frons in emargination of eye without yellow spot.

Head very finely and faintly striate, with irregular and often confluent punctures especially on clypeus and lower frons; vertex strongly striopunctate, central area of upper frons below vertex depressed; antennal segments 3 and 4 subcylindrical, 5 triangular, 6-10 rectangular (Fig. 131). Pronotum rough, finely and irregularly striate, tubercles indistinct except mp broad and rounded; gibbosity deeply divided (Fig. 129), anterior slope and sm tubercles deeply punctate. Mesoscutellum with central longitudinal carina



Figs. **128-131.** *Neochlamisus velutinus.* **128,** dorsal and lateral aspects; **129,** cephalic aspect; **130,** prosternum; **131,** antenna.

on anterior half sloping to depressed lateral margins, posterolateral margins reflexed. Metascutellum broadly exposed, longitudinally carinate. Elytra carinate, with many high tubercles (Fig. 128), coarsely and deeply punctate, anterior margins faintly crenate from scutellum to middle of humeral umbone except in front of ae tubercle; tubercles and carinae finely striate, high ae tubercle sloping to anterior margin, su-1a sharply carinate and connected with um-b; numerous deep punctures lateral and anterior to high, broad, and acute su-2, area between these punctures sharply carinate or spiny, ma carinate from humeral umbone to ma-a, su-3 high and elongated, ma-b area tumid; anterior 1/4 suture broadly open, exposing metascutellum, posterior 3/4 serrate. Pygidium covered with large, irregular, confluent or isolated shallow foveae with faint setigerous punctures; an

elongate depression near posterolateral border; central longitudinal carina broken; apical area flat. Prosternum (Fig. 130) slightly depressed in center, process slightly grooved longitudinally, posterior edge sloping steeply. Sternum covered with large, shallow foveae with faint setigerous punctures, foveae closer together than their diameters, producing reticulate appearance. First abdominal segment with process partly covering apex of femur and base of tibia in repose and forming lower edge of large depression; last segment with large, shallow, mid-ventral fovea; many short, lateral foveal hairs.

Aedeagus (Fig. 23) subtruncate, with transparent apical edge, slightly enlarged at middle; ejaculatory guide (Fig. 50) except for long sheath, slightly asymmetrical; basal orifice about 1/4 as long as ejaculatory guide.

Female allotype: 4.1 mm long; 3.2 mm wide. Color, sculpturing, and antennae similar to those of male. Mid-ventral fovea on last abdominal segment larger than in male, with hairs more numerous anteriorly. Spermatheca (Fig. 77) similar in general shape to that of other species in this genus.

Types: Male holotype, San Bernardino Ranch, Cochise Co., Arizona, 3750 ft., August, F. H. Snow (UK). Female allotype with the same data. Additional paratypes, all from Arizona: 1 ♂, Baboquivari Mts. (Pima Co.), 24 July 1941, Burt Hodgden; 1 ♂, Baboquivari Mts. (Pima Co.), 18 July 1932, R. H. Beamer; 1 ♂, Santa Rita Mts. (Pima Co.), 12 June 1933, R. H. Beamer; 1 ♂, Huachuca Mts. (Cochise Co.), 11 June 1933, R. H. Beamer; 1 ♀, Sierra Ancha Mts., Gila Co., no date, Duncan (UK). 1 ♂, 13 mi. S Ajo, Pima Co., 2 Apr. 1966, L. & C. W. O'Brien (JBK); 1 ♀, 8 mi. E San Vicente, 3000 ft., Pima Co., 8 Aug. 1954, F. G. Werner, L. Monrós collection, 1959 (USNM); 3 ♂ and 5 ♀, Santa Rita Range Reserve, Pima Co., 23 May 1957, 24 Apr. 1958, 29 Apr. 1958, 27 May 1958, G. Butler and F. Werner, swept mesquite (UAR); 1 ♂ and 4 ♀, Canelo, Pyeatt's Ranch, (Santa Cruz Co.), 28 May 1953, A. & H. Dietrich (CU); 1 ♀, Portal (Cochise Co.), 17 June 1956, H. & A. Howden (HFH); 2 ♂ and 3 ♀, Sabino Canyon, Tucson (Pima Co), 16 May 1953, A. & H. Dietrich (CU); 3 ♂ and 3 ♀, Sabino Canyon (Pima Co.), 11 July 1949, 30 July 1950, 4 June 1951, 11 July 1952, D. J. & J. N. Knull (OSU); 2 ♂ and 2 ♀, Tucson (Pima Co.), 27 July 1936, 13 Aug. 1936, J. N. Knull (OSU, JAW); 1 ♂ and 3 ♀, Tucson (Pima Co.), 18 May 1953, 20 May 1953, A. & H. Dietrich (CU); 1 ♂, 10 mi. N Tucson (Pima Co.), 25 Apr. 1957, G. D. Butler, swept alfalfa (UAR); 1 ♂, 15 mi. E Tucson, Pima Co., 6 June 1952, M. Cazier, W. Gertsch, and R. Schammel (AMNH).

Discussion: Most references to *memnonius* in North America and Mexico refer to *velutinus*. An examination of the female syntype of *memnonius* in the British Museum reveals several differences between the two species as pointed out in the above key. The determined series in the same collection, specimens of which were referred to in Biologia Centrali-American (Jacoby 1881, 1889) contain both species including specimens of another species, *moestificus*. The name *velutinus* describes the appearance of the spots on the elytra.

Males vary in length from 3.6-3.9 mm and in width from 2.7-3.0 mm; length of females varies from 3.8-4.2 mm and the width from 2.8-3.2 mm.

The color is dark brownish to dark reddish bronze, with small areas of metallic blue, purple, or red reflections.

N. velutinus more closely resembles *memnonius* than it does the other three species of the group. The close relationship of these two species is further suggested by the similar ejaculatory guides, which differ in size and shape from the others in the group. The much smaller velvety spots on the elytra and the shape of the aedeagus serve to separate *velutinus* from *memnonius*. In the development of the pronotal gibbosity and of the velvety spots of the elytra, *velutinus* is intermediate between *moestificus* and *memnonius*. The sculpturing of *velutinus* varies considerably but generally follows that found in the genus as a whole as to the number, position and size of punctures and tubercles. The coloring is similar to that of *moestificus*.

The highly developed metascutellum is broadly exposed, similar to that found in the other species of the group except *moestificus* in which it is definitely smaller and almost to completely covered by the often closed elytral suture.

The specimens which I have seen from Chihuahua, Nayarit, Sinaloa, and Sonora, Mexico, are mostly females, with tibial spines very small or lacking on the front and middle legs. Their elytra are less tuberculate than those of most Arizona specimens but not unlike some found in samples from Arizona and Baja California. There is one male from Guaymas, Sonora, Mexico, associated with these females, and since it is similar to the Arizona specimens, both it and the females have been included in *velutinus*.

Plant records: Several different series without larvae have been collected on *Prosopis glandulosa*. Only single specimens have been found on *Acacia constricta, Neltuma glandulosa, Prosopis chilensis* and alfalfa.

Specimens examined (89 males and 140 females): (Map 4)

UNITED STATES: ARIZONA: Cochise Co., 4-17 June, Aug., 14 Sept., 29 Sept.; Gila Co., 20 June, 18 July, 7 Aug.; Graham Co., 27 Apr., May, June, 4 July, 10 Aug.; Maricopa Co., 13 Sept.; Navajo Co., 21 June; Pima Co., 2 Apr., 24 Apr.-12 June, 3 July-13 Aug.; Pinal Co., 26 July; Santa Cruz Co., 3 Apr., 28 May, 28 June, 14 July, 29 July. TEXAS: Bexar Co., 6 Apr., 23 Aug.; Cameron Co., 25 Mar., 17 Apr., 6 May, 23-25 June, 22 July-8 Aug.; Comal Co., no date; Duval Co., 18 Mar., 23 Apr.-4 May, 31 May; Hidalgo Co., 20-26 Mar.; Kinney Co., 27 Aug.; La Salle Co., 29 June; Presidio Co., 20 June; San Patricio Co., 28 Mar.; Starr Co., 28 Mar.-9 Apr., 2 June; Uvalde Co., 23 May, 14 June, 30 June, 4 Aug., 25 Aug.; Val Verde Co., 25 Apr.-5 May; Webb Co., 27 June; Zapata Co., 21 May.

MEXICO: BAJA CALIFORNIA: San Fernando, 31 July; Bahía de Los Angeles, 15 May; Mesquital, 28 July. BAJA CALIFORNIA SUR: San Ignacio, 26 June; 15 mi. N El Refugio, 4 July; Triunfo, 13 July; 15 mi. N San Ignacio, 26 June; 45 mi. N San Ignacio, 27 June; Vanancio, 17 July; Santo Domingo, 19 July. CHIHUAHUA: Chihuahua, no date; 92 km. N Chihuahua, 30 June. COAHUILA: Boqillas del Carmen, 23 May. GUERRERO: Río Balsas, no date. MORELOS: Puente de Ixtla, no date. NAYARIT: Jesús María, 26 June; 2 mi. S Acaponeta, 21 Mar. NUEVO LEON: Apodaca, 27 July. SAN LUIS POTOSÍ: 46 mi. N San Luis Potosí, 1 Sept. SINALOA: 32 mi. S Mazatlán, 22 June; 20 mi. E Villa Unión, 19 Aug. SONORA: Guaymas, 3 June; Magdalena, 23 July; 4.9 mi. N Magdalena, 25 Aug.; Yecora, 20-22 May.

Neochlamisus memnonius (Lacordaire)

Chlamys memnonia Lacordaire, 1848:708-709 (misspelled menmonia[5]).
Diaspis memnonia (Lacordaire); Baly, 1878:343.

Diagnosis: The large, distinct velvety spot on each elytron, high pronotal gibbosity with deep medial groove, acute tubercles and carinae, broadly exposed metascutellum, and the absence of a yellow spot on the frons in the emargination of the eye serve to distinguish this species.

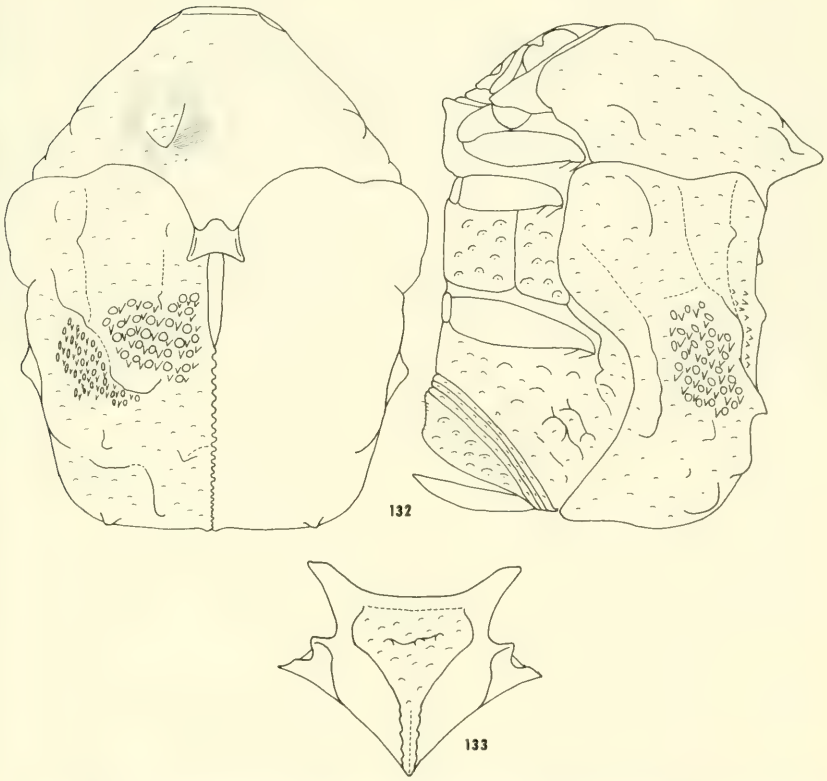
Description: Male: 3.0-3.9 mm long; 2.7-3.3 mm wide. Female: 4.0-4.5 mm long; 2.8-3.2 mm wide. Dark to reddish bronze in color. Antennae yellowish brown, apical half of last segment dark; labrum with dark brown apical border; frons without yellow spot in emargination of eye.

Head finely and faintly punctate, except vertex moderately punctate; antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum moderately striate, with large areas nonstriate and granulate, faintly and finely punctate; mp tubercle small, nonstriate, la and su forming high gibbosity, moderately striate, coarsely to moderately punctate; anp absent; gibbosity deeply divided, posterolateral slopes irregularly striate and coarsely punctate, posterior lobes nonstriate and impunctate. Mesoscutellum granulate, lateral margin with small dorsal ridge, posterolateral angles reflexed. Metascutellum broadly exposed. Elytra (Fig. 132) coarsely to moderately punctate, anterior tubercles acute and carinae sharp; large, confluent, discal, velvety spots separated by sharp carina from broad su-2 to small su-1a tubercles; anterior 1/5 or more of elytral suture open, broadly exposing metascutellum, posterior 4/5 serrate. Pygidium with smooth, medial carina; foveae confluent except in center next to carina. Prosternum (Fig. 133) about 1 1/2 times as long as wide. Last abdominal segment with large, granulate fovea; fovea deeper in female and with fewer scattered hairs than in male. Well developed single spine on front and middle tibiae in male; no tibial spine in female.

Aedeagus (Fig. 21) explanate with transparent apical edge; ejaculatory guide (Fig. 51) more than six times as long as wide, sheath slender, basal orifice 1/5 total length of ejaculatory guide. Spermatheca (Fig. 78) J-shaped, apex of cornua slightly enlarged.

Types: Lacordaire apparently based his description on two females, one from the Dupont collection and the other from Pilate, who collected it in the environs of Campeche, Yucatan, Mexico. I have not been able to locate the Dupont specimen; it is assumed to be lost. The Dupont syntype could be in one of a number of collections, but probably ought to be either in the Paris Museum or in the Bowditch collection at the Museum of Comparative Zoology, Harvard. An examination of this latter collection failed to locate

[5] In the "table alphabetique," page 879 of Lacordaire's monograph, this species is indexed as *memnonia.* The spelling in the text is therefore an obvious misspelling.



Figs. 132-133. *Neochlamisus memnonius.* 132, dorsal and lateral aspects; 133, prosternum.

the specimen. Material from the Paris Museum marked as part of the R. Oberthür collection to which Dupont's specimens are said to have gone, did not contain this type.

A female specimen in the British Museum (Natural History) is without doubt the syntype from Pilate's collection and agrees very well with Lacordaire's description, except that he makes no mention of the broadly exposed second scutellum. It is as obvious as the second scutellum of *Diplacaspis paradoxa;* therefore, it is remarkable that it was overlooked by Lacordaire. This syntype is designated as the lectotype. It has the following label data: Cotype; 5; Baly coll.; *Chlamys memnonia* Lac. type, type ex coll. Pilate; *Chlamys memnonia* Lac., 5, C. Yucatan, N. S.; *Diaspis memnonia* Lac., Yucatan, ex coll. Deyolle. The specimen is 4.0 mm long and 2.8 mm wide.

Discussion: This species is included because of its close relationship to *velutinus,* with which it has been confused by earlier authors. The form commonly recognized as *memnonius* in the United States is *velutinus.* The

reference to *Chlamys mimnonius* (misspelling) by Fall (1927) probably refers to *velutinus*. The specimens from Mexico referred to by Pallister (1953) as *Chlamisus memnonius* are *moestificus*. There were four misidentified specimens of this genus in the British Museum labeled *memnonius*. Two of them are *velutinus* and two are *moestificus*. All but one were referred to as *memnonius* by Jacoby (1889) in the Biologia Centrali-Americana.

Jacoby (1881), after examining the Pilate type from Baly's collection, felt that Lacordaire overlooked the second scutellum in this species. Jacoby and Baly placed *memnonius* in the genus *Diaspis*, but I have already discussed in the generic treatment my reasons for not including this species and several others in that genus.

The large velvety elytral spots so distinctive in this species probably are a specialized condition, and the other species of this group represent intermediates. The smooth punctate condition of the corresponding area of the elytra which is retained in most of the *gibbosus* species group probably is a more primitive condition. Likewise the loss of the yellow spot on the frons in the emargination of the eye represents a specialized condition, as compared to the more primitive one of a yellow spot or an even earlier condition of a completely yellow face.

Plant records: The close relationship of this species to *velutinus* is reflected in the host plants, both being found on legumes. At present the major host of *memnonius* is not definitely known, but it is probably a species of *Prosopis*. The one female examined is mounted with the larval case from which it emerged. This case is attached to a small thorny twig characteristic of some species of *Prosopis*. The case has no indication of plant hairs being used in its construction (cf. larvae of *moestificus*). It does show various dark and light annulations which indicate that several different materials were used in its construction.

Specimens examined (six males and three females): (Map 4)

MEXICO: CAMPECHE: Environs of Campeche (lectotype). GUERRERO: Acapulco, no date; Chilpancingo, no date. JALISCO: 17 mi. W Guadalajara, 5000 ft., 11 Aug., pupa on legume; Plan de Barrancas, 24 Aug. OAXACA: Tehuantepec, 18 July; Rincon Antonio, no date. PUEBLA: 10 mi. SE Izúcar de Matamoros, 19 June, on legume.

Neochlamisus moestificus (Lacordaire)

Chlamys moestifica Lacordaire, 1848:706-708.
Diaspis moestifica (Lacordaire); Jacoby, 1881:75.
Chlamys confusa Schaeffer, 1919:325.
Boloschesis moestifica (Lacordaire); Schaeffer, 1926:185-186.
Chlamisus moestifica (Lacordaire); Blackwelder, 1946:649.

Diagnosis: This species has a very narrowly exposed metascutellum, small velvety elytral spots, distinct elytral punctures, striopunctate and tu-

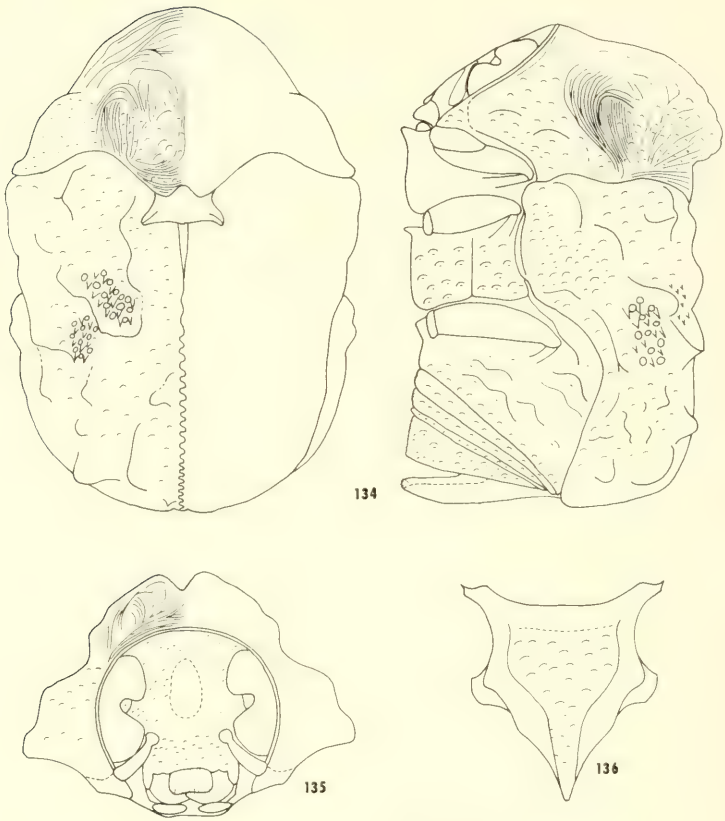
berculate pronotum, smooth and granulate mesoscutellum, and large, often sharply carinate elytral tubercles.

Description: Male: 3.2-3.9 mm long; 2.3-3.8 mm wide. Female: 3.3-4.5 mm long; 2.2-3.1 mm wide. Color dark brownish to bright reddish bronze. Antennae yellowish brown at base, becoming darker brown at apex; frons with small to large yellow spot in emargination of eye.

Head mostly finely and faintly punctate, more coarsely punctate between antennal sockets and on vertex, vertex finely and faintly striopunctate. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular, segments 4 and 5 slightly smaller in female than in male. Pronotum rough, finely and regularly striate; mp, la, and su tubercles coarsely punctate, producing rough appearance, other areas faintly punctate, anp tubercle faint; gibbosity moderately divided (Fig. 135), posterolateral slopes striopunctate; posterior lobes transversely, finely striate, with scattered punctures. Mesoscutellum granulate, posterior margin flat to slightly depressed, posterolateral corners reflexed slightly. Metascutellum barely visible between elytra. Elytra (Fig. 134) with large tubercles and carinae, moderately punctate, anterior tubercles sharply carinate; each discal velvety spot distinct, consisting of 6-12 deep punctures separated by sharp ridges; su-2 slightly crescent-shaped; elytral suture narrowly exposing metascutellum. Pygidium with smooth medial carina, foveae usually confluent. Prosternum (Fig. 136) nearly twice as long as wide. Last abdominal segment with large, granulate, slightly depressed mid-ventral fovea; fovea more depressed, and with hairs more scattered in female than in male. Well developed spine on front and middle tibiae; tibial spines usually smaller and less curved in female than in male.

Aedeagus (Fig. 22) subtruncate to explanate, with small transparent apical edge; ejaculatory guide (Fig. 52) short and robust, length five times width; basal orifice 1/5 as long as ejaculatory guide. Spermatheca (Fig. 79) J-shaped, apex of cornua slightly enlarged.

Types: There is one male specimen in the British Museum with the following label data: E. Coll. Laferte; D.; Cotype; *C. moestifica* Lac.; 6756; *Chlamys subaenea* Reiche, Mexico. This specimen may or may not be one of Lacordaire's syntypes. He had many examples from the collection of Dupont from which he described two varieties of *moestificus.* Lacordaire based several species in part on material from both the Laferte and Reiche collections, but he did not mention these collectors in the description of *moestificus.* No other types have been found in the following museums where Lacordaire's or Dupont's specimens might be located: Museum National d'Histoire Naturelle, Paris; Institut Royal des Sciences Naturelles de Belgique, Bruxelles; Museum of Comparative Zoology, Harvard University; Museum Alexander Koenig, Bonn. The specimen in the



FIGS. **134-136.** *Neochlamisus moestificus.* **134,** dorsal and lateral aspects; **135,** cephalic aspect; **136,** prosternum.

British Museum is accordingly accepted as a type until there is evidence to the contrary. It is not being designated as the lectotype since there is some question about its identity, and there is no question about the identity of the species.

Discussion: This is the most variable species in the *velutinus* group. It also seems to accept a variety of host plants. The color is generally dark with some metallic reflection. All the examples I have from Utah, however, are dark to bright reddish bronze. They also are larger and more carinate than the majority of the specimens seen from other localities. Many specimens from this Utah locality have a small, almost imperceptible yellow spot on the frons in the emargination of the eye. They may be confused with *velutinus,* but the latter species is much darker and more tuberculate. The prosternal process and the ejaculatory guide are much shorter in relation to the width in *moestificus* than in *velutinus.*

Occurrence of different populations on separate host plants suggests that two or more species are involved. The following evidence for *moestificus* indicates one highly variable species, possibly with some populations in an active state of speciation. Even though samples with fairly consistent differences have been taken from two species of *Eriogonum* and one species of *Polygonum,* the differences are not consistent enough to warrant separate status at the species level. For example, the shape of the aedeagus is fairly uniform in the Utah sample of *moestificus,* but among males from other localities, the shape varies, including the two examples illustrated and many intermediates. The Arizona samples from *Eriogonum* and *Polygonum* show this range of aedeagal variation but are fairly uniform in sculpturing. Other samples from Arizona show a range of variation in both sculpturing and shape of the aedeagus; so it is impossible to distinguish more than one species.

One of the most obvious morphological variations is the size of the scutellar tubercle. In the Utah forms it is usually large and sharply carinate, with tubercle su-1 present. In several Arizona samples this tubercle is almost absent, with no trace of a carina, su-1 is small, and the other elytral tubercles are reduced in size. In the specimens with abbreviated tubercles, the punctures are very distinct and sparse, and the apex of the aedeagus is usually similar to that found in the Utah examples. Although this type of sculpturing and punctation is fairly consistent in samples from one or two localities, some highly tuberculate specimens also have the distinct, sparse punctures.

The character of distinct punctures used by Schaeffer (1926) to distinguish *moestificus* from *scabripennis* is valid for the majority of the specimens examined, but the larger and more exposed metascutellum found in *scabripennis* is a more useful character in separating these two species. In *moestificus* the exposure of the metascutellum is always slight and in many cases there is almost no exposure. I have seen examples from several different localities with punctation very similar to that of *scabripennis,* but the specimens are darker and the metascutellum scarcely exposed. On the basis of these characters, the distribution, and the host information, I consider them variants of *moestificus.*

Additional and more accurate information on host plants and distribution may reveal one or more sibling species in what I choose to recognize as *moestificus.* The widely distributed eastern samples are usually only single specimens. Information from such samples is more tentative than that from the Southwest where more extensive samples are available. It appears that this species is undergoing the most active evolution in the species group. The present study suggests that *subelatus* and *scabripennis* are more recently separated from the *moestificus* line of evolution than are

memnonius and *velutinus*. They have reached a level of differentiation that deserves species recognition on the bases of the morphological and ecological characters mentioned in the respective species discussions.

Plant records: Eriogonum racemosum (series with larvae), *E. wrighti?* (series with larvae), *E. microthecum, Polygonum* sp. (series with larvae), *Ceanothus fendleri* (series with larvae), and *C. buxifolia*.

Parasites: No parasites have been identified, but larvae of parasitic Hymenoptera have been found in pupal cases of this species collected in the field.

Immature stages: The following information is derived mostly from material collected in Utah County, Utah, on *Eriogonum racemosum*. Comparisons were made with larvae and adults taken on *Ceanothus fendleri* near Flagstaff, Arizona. Adults of *N. moestificus* were collected together with larvae and pupae near Provo, Utah, on the host plant. In a few instances pupae and adults were picked from grass or other plants in the vicinity; however, on the basis of observations of feeding and the type of pubescent material used in the construction of the larval case, the *Eriogonum* is considered the only host in this instance. It is quite common for adults, and even mature larvae ready to pupate, to wander to plants other than the hosts. Such records cause considerable confusion when one is trying to determine actual hosts.

The larvae and pupae, like the adults, are very difficult to find, but for a different reason. The use of plant pubescence in the fecal case makes it very similar in texture to the plant stem and difficult to see. The construction of this case indicates that the larva incorporates several types of material into it. This reflects feeding on the leaves, stems and even the flowers at different times during larval development. Overall, the case is black to dark brown, with some light brown annulations as well as sections incorporating large amounts of pubescence. The original egg case is attached to the apex and is of a different texture and color, as might be expected.

The larvae are generally found near the base of the plant where most of the leaves occur. The mature larvae pupate by attaching the fecal case firmly to a major stem of the plant, usually in or near a furcation. The case is situated so that the apex points down and away from the stem. If the original egg covering from the female has not been broken from the larval case, it is situated parallel to the stem and appears as an apical appendage on the case. Inside this larval case are the discarded exuviae of the earlier instars compressed into the apex. Upon emerging from the pupal skin the adult remains inside the case until its cuticle has darkened and hardened. With its mandibles it then cuts a circular incision near the apex of the case and crawls out. I suppose that mating does not take place

until the following spring since only one generation a year has been observed, and adults collected in the spring readily mate in the laboratory while those collected in August do not.

Ecological notes: The adults although brightly colored are usually difficult to see because of their small size and their habits. The *Eriogonum* plant itself, although 2-3 feet in height, is difficult to see from a distance since the leaves are basal and the stems are very slim. The adults of the beetles usually appear as dark objects along the silvery stems. They quickly drop to the ground when disturbed. They can be collected easily by placing a net beneath the plant, then gently touching the stem. On warm days the adults have a tendency to fly rather than drop to the ground; then sweeping is an effective means of collecting.

Specimens examined (159 males and 263 females): (Map 5)

UNITED STATES: ARIZONA: Cochise Co., 3 June, 14-20 June, 5 July-19 Aug., 7 Sept., 19 Sept.; Coconino Co., 19-25 June, 13-14 July, 8-15 Aug.; Gila Co., May, 14-17 June, 12 July-Aug., 10 Sept.; Graham Co., 10 May, 19 July, 9 Aug.; Navajo Co., 19 June, 1 May, 6 July, 18-20 July; Pima Co., 12 June, 10-26 July, 1 Aug., 18 Aug., 1-3 Sept., 24 Sept.; Pinal Co., 4 Sept.; Santa Cruz Co., 10 June, 6-7 Sept.; Yavapai Co., 10-30 June, 29 July-3 Aug.; Yuma Co., 20 May. ARKANSAS: Benton Co., 11 Aug. COLORADO: Archuleta Co., 22-24 June; Larimer Co., 14 Aug. FLORIDA: Broward Co., Apr.; Duval Co., no date; Volusia Co., no date. GEORGIA: Haralson Co., 19 June. ILLINOIS: Union Co., 7-11 Aug. KANSAS: Riley Co., June. KENTUCKY: state record, no date. MARYLAND: Montgomery Co., summer. NEW MEXICO: Catron Co., 23 June; Grant Co., 23 July. NEW YORK: Albany Co., 4 Oct.; Westchester Co., 5 July. OREGON: Wheeler Co., 9 Sept. SOUTH CAROLINA: Oconee Co., 25 May. TEXAS: state record, no date. UTAH: Utah Co., 30 July, 22-23 Aug.

MEXICO: CHIHUAHUA: Chihuahua, no date. DURANGO: Palos Colorados, 5 Aug.; 24-36 mi. W Durango, 4-6 May, 6-9 June, 2-7 July, 21 July; 28 mi. E El Salto, 22 July. GUERRERO: Omilteme, July. OAXACA: Juquila, no date. PUEBLA: Environs of Puebla, no date. SONORA: Yecora, 20-22 May.

Doubtful locality: 1 female in the Paris museum labeled "Brazil."

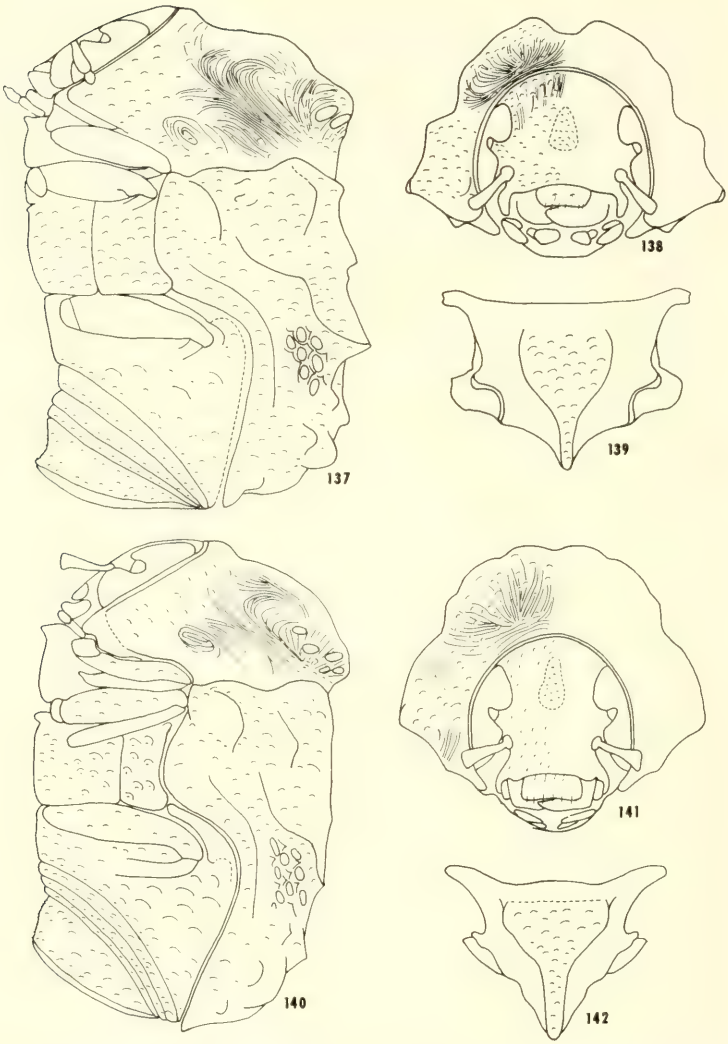
Neochlamisus scabripennis (Schaeffer)

Boloschesis scabripennis Schaeffer, 1926:184-185.
Chlamys scabripennis (Schaeffer); Leng and Mutchler, 1933:44.

Diagnosis: Characters used to identify this species are the bright reddish bronze color, distinctly striate pronotum, moderately divided pronotal gibbosity, large, confluent elytral punctures, broadly exposed metascutellum and coarsely striate, rugose mesoscutellum. Many of the elytral punctures, tubercles and carinae are vertically striate. The area between punctures is shiny granulate or striate.

Description: Male: 3.5-3.8 mm long; 2.5-2.8 mm wide. Female: 3.6-4.6 mm long; 2.7-3.3 mm wide. Antennae yellowish brown, becoming darker brown at apex; mandibles reddish brown; frons with large yellow spot in emargination of eye.

Head finely and faintly punctate except moderately punctate on vertex. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular, segments 4-6 slightly smaller in female than in male. Pronotum finely punc-



FIGS. **137-139.** *Neochlamisus scabripennis.* **137,** lateral aspect; **138,** cephalic aspect; **139,** prosternum. FIGS. **140-142.** *Neochlamisus subelatus.* **140,** lateral aspect; **141,** cephalic aspect; **142,** prosternum.

tate, finely to moderately and regularly striate along contours; mp tubercle small, other tubercles merged with large, rough, moderately punctate and moderately divided gibbosity (Fig. 138); posterolateral slopes striopunctate, striations converging at base; posterior lobes transversely, moderately striate with few punctures. Mesoscutellum coarsely granulate, posterior margin depressed, posterolateral corners reflexed and faintly striate. Metascutellum

well developed, broadly exposed between elytra. Elytra (Fig. 137) with large blunt tubercles and sharp carinae, coarsely punctate, granulate; tubercles, carinae and punctures obscurely striate; discal velvety spots obscure, consisting of 15-20 deep punctures separated by sharp ridges, su-2 broad and acute, carinate with su-1a and umbone, sc carinate to su-1. Pygidium with smooth medial carina, foveae largely confluent and granulate. Prosternum (Fig. 139) nearly twice as long as wide. First abdominal segment with hairs posterior to large mid-ventral carina; last segment with large smooth depressed mid-ventral fovea, punctation mostly confluent, foveal hairs sparse on anterior and posterior border of sternum, lateral areas impunctate to finely punctate. Well developed spine on front and middle tibiae of both sexes.

Aedeagus (Fig. 24) explanate, with transparent apical edge; ejaculatory guide (Fig. 53) short and robust, length about three times width, sheath broad. Spermatheca (Fig. 80) U-shaped, cornua slightly enlarged; collum bulbular with blunt-pointed apex.

Type: Male holotype, Marathon (Brewster Co.), Texas, 7 June, 1908; Mitchell and Cushman coll.; *scabripennis* type, USNM 29464. The type is not brightly colored, and the dull metallic reflections are more purplish or reddish than in most specimens.

Discussion: Although Schaeffer listed paratypes from New Mexico, Arizona, and California, I have not seen any examples from further west than extreme southeastern Arizona. I also have one male and one female labeled "Lakewood, N.J.," a locality far removed from the normal distribution of this species. I consider these specimens mislabeled.

This species is fairly uniform in size, color, and sculpturing, but as in other species in this species group, there are some differences in the size and shape of tubercles, placement of punctures, and brightness of the color. It is similar to *subelatus* in color but very different in sculpturing, in which it more closely resembles *moestificus*.

The shape of the aedeagus and ejaculatory guide is fairly consistent in the specimens examined. The aedeagus might be considered intermediate between the extremes illustrated for *moestificus*, so that on this basis alone one could not distinguish any specimens.

Plant records: "Grease-wood" (series), (probably *Sarcobatus vermiculatus; Larrea* is sometimes called greasewood in Arizona); *Larrea divaricata* (series).

Specimens examined (38 males and 30 females): (Map 6)

UNITED STATES: ARIZONA: Cochise Co., 27 June, 9-25 July. NEW MEXICO: Dona Ana Co., 22 June. TEXAS: Brewster Co., 7 June, 1-2 July; El Paso Co., 15 June, 8-9 July; Presidio Co., 4-30 Apr., 6-8 Aug.; Terrell Co., 27 Apr.; Val Verde Co., 27 Aug.

MEXICO: CHIHUAHUA: 3 mi. W Jiménez, 26 July. SAN LUIS POTOSÍ: 46 mi. N San Luis Potosí, 1 Sept. ZACATECAS: 10 mi. N Fresnillo, 10 May.

Neochlamisus subelatus (Schaeffer)

Boloschesis subelata Schaeffer, 1926:184.
Chlamys subelata (Schaeffer); Leng and Mutchler, 1933:44.

Diagnosis: This is the least tuberculate species of the group. It appears rugose because of the broad striae and punctures on the elytra and has a consistently bright reddish bronze color. The metascutellum is always widely exposed, and the pronotal gibbosity is slightly divided.

Description: Male: 3.5-3.8 mm long; 2.4-2.8 mm wide. Female: 3.6-4.3 mm long; 2.6-3.0 mm wide. Dark reddish to bright reddish bronze. Antennae light brown; frons with large yellowish brown spot in emargination of eye.

Head moderately punctate on clypeus and between antennal sockets, coarsely punctate and finely striate on vertex, rest finely punctate; depressed medial area on upper frons usually large and deep. Antennal segment 4 subtriangular, 5 subquadrate, 6-10 rectangular, segments 4-5 smaller in female than in male. Pronotum finely to moderately and regularly striate along contours; mp tubercle large, evenly rounded, finely punctate; la, anp and su tubercles small and merging with evenly rounded, slightly divided, coarsely punctate gibbosity (Fig. 141); posterolateral slopes faintly striopunctate; posterior lobes moderately striate, with scattered punctures. Mesoscutellum coarsely granulate and moderately striate, posterior margin gradually depressed, posterolateral corners rounded and slightly reflexed. Metascutellum broadly exposed between elytra. Elytra (Fig. 140) with small rounded tubercles and sharp carinae, coarsely punctate, area between punctures usually shiny; faint discal velvety spots consisting of 6-12 deep punctures separated by sharp ridges, su-2 crescent-shaped and carinate to su-1a and umbone, ae broadly rounded, sc carinate with su-1; 2-3 coarse, short, longitudinal striae between su and mesoscutellum. Pygidium with smooth medial carina; many large shallow foveae near carina. Length of prosternum (Fig. 142) less than twice width. First abdominal segment faintly carinate on posterior half between coxae, with large setigerous punctures; last segment with flat to slightly depressed mid-ventral fovea, foveal hairs sparse. Mid-ventral foveal area large, more depressed in female than in male, lateral hairs numerous. Well developed spine on front and middle tibiae in both sexes.

Aedeagus (Fig. 25) subtruncate to explanate, with short transparent apical edge; ejaculatory guide (Fig. 54) short and robust, length about three times width. Spermatheca (Fig. 81) slimmer than that of other species in the genus; apex of cornua slightly enlarged, collum bluntly pointed.

Types: Schaeffer based his description on specimens reared from larval cases taken on *Larrea tridentata* at Tucson (Pima Co.), Arizona. One female collected 23 February 1897 on *Larrea tridentata* is the holotype

(USNM, cat. no. 29463). There are also two female paratypes from the Hubbard and Schwarz collection labeled Jan. and Feb. 1897 (USNM).

Discussion: Although the body coloring and one of the host plants are the same as for *scabripennis,* there is little chance of confusion of the two because of the difference in sculpturing. The geographical distributions of these species do not overlap, except in eastern Arizona. As is usually the case in *Neochlamisus,* there is considerable variation in the shape of tubercles and carinae, and especially in the placement of punctures. This variation, however, does not cause any problems in identification of the species.

As in *scabripennis,* the shape of the aedeagus and the ejaculatory guide of *subelatus* is intermediate between the two extremes described for *moestificus.* This indicates the close relationship of the three species.

Plant records: Larrea tridentata glutinosa (series with larvae) and *L. divaricata* (series).

Specimens examined (71 males and 102 females): (Map 6)

UNITED STATES: ARIZONA: Coconino Co., Aug.; Gila Co., no date; Mohave Co., 28 Apr., 16-20 July, 15 Sept.; Maricopa Co., 9-11 May, 16 June, 29 June-6 July, 31 Aug., 19 Sept.; Pima Co., 16 Feb., 9 Apr., 4 May, 8-16 June, 6 July-10 Aug., 24 Sept., 31 Dec.; Pinal Co., 21 Aug., 19 Sept.; Yavapai Co., 14 June, 25 July; Yuma Co., 14 Mar., 16 June. CALIFORNIA: Imperial Co., 10 Jan.; Inyo Co., 7 June; Kern Co., 25 Apr., 1-6 June; Los Angeles Co., 11 Aug.; Riverside Co., Apr., 21 May, 25 June, 14 Oct.; San Bernardino Co., 25-30 Mar., 9-11 Apr., 26 Apr., 5-11 June, 14 Sept.; San Diego Co., 25 June, 6 July, 20 July, 7-12 Aug., 17 Sept. NEVADA: Clark Co., 9 Sept., 6 Nov.; Lincoln Co., 15 July, 24 Nov.; Nye Co., 31 May, 10-16 Aug.

MEXICO: SONORA: Altar, 9 May; Guaymas, 3 June.

gibbosus Group

This species group includes *gibbosus* and eleven related species formerly included in the genus *Chlamisus.* One additional species is described as new.

This group includes those species of *Neochlamisus* with an asymmetrical ejaculatory guide, an incompletely serrate but closed elytral suture, and without large velvety spots on the elytra (small velvety spots on *bimaculatus*).

The species of the *gibbosus* group are found from Mexico to eastern Canada on diverse and numerous host plants. The species are much less restricted to a particular host than those of the *velutinus* group. The close relationship of the two species groups of *Neochlamisus* is illustrated by the form of the aedeagus and ejaculatory guide, the number of tibial spines and faint indications of velvety elytral spots in several species of the *gibbosus* group.

Key to the *gibbosus* Species Group

1a. Last abdominal segment and pygidium usually roughly sculptured but not vermiculate 3

b. Last abdominal segment and pygidium vermiculate 2

2a. Single spine on front tibia of male ..... *fragariae*
b. Two spines on front tibiae of male ..... *eubati*
3a. Pronotal gibbosity deeply divided; prosternal process usually serrate in male 4
b. Pronotal gibbosity feebly or moderately divided; prosternal process not serrate in either sex 8
4a. Males with two unequal spines on front tibia; females without tibial spines; aedeagus broadly truncate; posterolateral slopes of pronotum coarsely and regularly striate ..... *gibbosus*
b. Males with two subequal spines on front tibia; females with or without tibial spines; aedeagus not broadly truncate; posterolateral slopes of pronotum finely to coarsely and irregularly striate 5
5a. Small or faint velvety spots on elytra; females without tibial spines; abdominal segments not foveolate ..... *bimaculatus* n. sp.
b. No velvety spots on elytra; females with spine on front and middle tibiae; abdominal segments foveolate 6
6a. Elytra with numerous, usually noncarinate tubercles ..... *insularis*
b. Elytra with normal tubercles and carinae 7
7a. Color bright yellowish bronze; posterolateral slopes of pronotum usually finely striate, striae usually convergent; pygidium foveolate ..... *platani*
b. Color dark brownish bronze; posterolateral slopes of pronotum moderately and irregularly striate; pygidium punctate ..... *bebbianae*
8a. Single spine on anterior and middle tibiae of males; similar but smaller tibial spines in female ..... *chamaedaphnes*
b. Two spines on anterior tibia, single similar spine on middle tibia of males; females with or without tibial spines 9
9a. Prosternum subtriangular, sides evenly convergent anteriorly or slightly emarginate 10
b. Prosternum goblet-shaped, sides strongly emarginate 11
10a. Anterior slope of pronotum obscurely striate; first abdominal segment impunctate, pygidium obscurely foveolate ..... *tuberculatus*
b. Anterior slope of pronotum finely striate, first abdominal segment impunctate, pygidium moderately to coarsely punctate ..... *cribripennis*
11a. Spines absent from anterior and middle tibiae of females ..... *comptoniae*
b. Spines present on anterior and middle tibiae of females ..... *assimilis*

Neochlamisus gibbosus (Fabricius)

Bruchus gibbosus Fabricius, 1776:212.
Clythra plicata Fabricius, 1798:111-112.
Chlamys plicata (Fabricius); Olivier, 1808:876.
Chlamys gibbosa (Fabricius); Gemminger and Harold, 1874:3303.
Boloschesis gibbosus (Fabricius); Schaeffer, 1926:187.
Arthrochlamys plicata (Fabricius); Brown, 1943:127-128.
Chlamisus gibbosa (Fabricius); Proctor, 1946:186.
Chlamisus plicata (Fabricius); Fattig, 1948:8.
Arthrochlamys gibbosa (Fabricius); Jaques, 1951:275.

Diagnosis: The large size, moderately and regularly striate posterolateral slopes of the pronotum, large elytral tubercles, truncate aedeagus, strongly serrate prosternal process in males, two unequal spines on the front tibiae

of males and absence of spines from front and middle tibiae in females characterize this species.

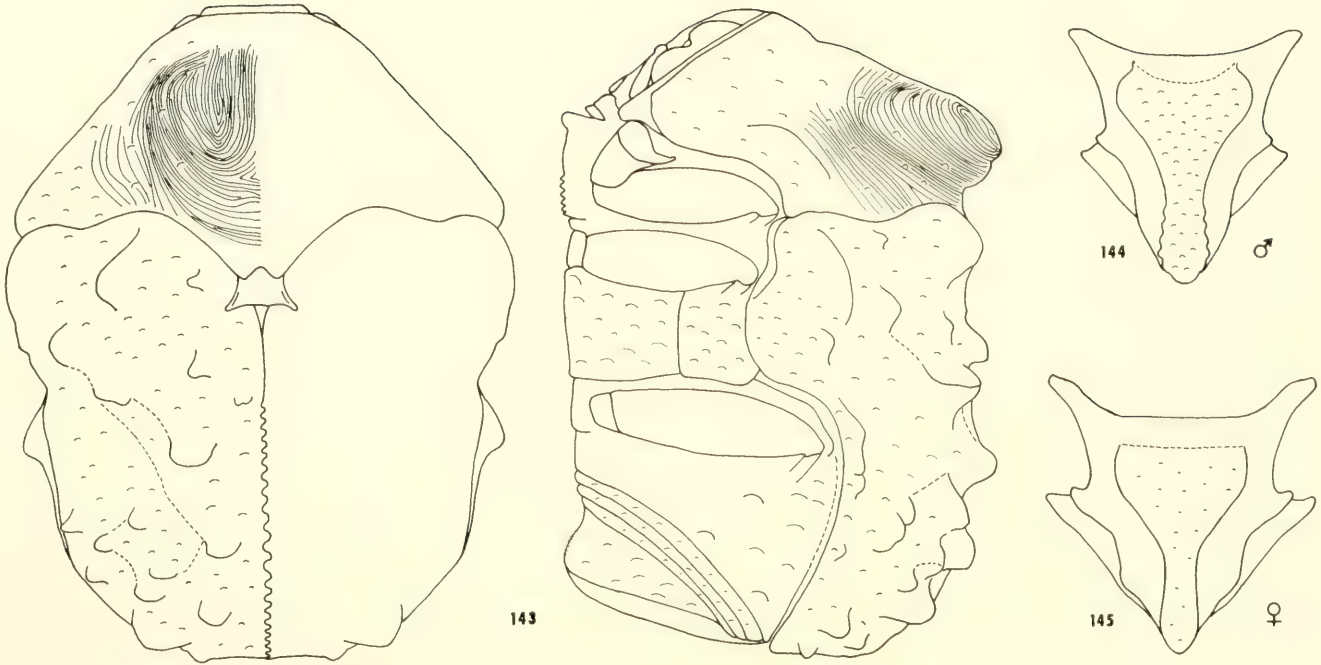
Description: Male: 4.5-4.8 mm long; 2.6-3.7 mm wide. Female: 4.2-4.9 mm long; 3.1-3.8 mm wide. Color dark brownish to bright reddish or yellowish bronze. Antennae yellowish brown; frons with large yellow spot occupying about 1/2 of emargination of eye.

Head finely and faintly punctate, large fovea on lower frons near ventral edge of antennal socket; lower frons and vertex usually with strongly depressed central area. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum regularly moderately striate, tubercles faint or absent, impunctate; gibbosity deeply divided; posterior lobes transversely and finely striate. Mesoscutellum granulate, posterior margin flat to faintly depressed, posterolateral corners reflexed slightly. Elytra (Fig. 143) finely but deeply punctate, with large tubercles and carinae; su-3 large, longer than broad, ma-b obliquely carinate, ma longitudinally carinate along lateral margin, anterior tubercles round, su-1a faintly carinate. Pygidium finely and faintly punctate, with smooth medial carina; large shallow foveae mostly confluent. Prosternum (Fig. 144) more than twice as long as wide, posterior half of process explanate, grooved and serrate in male; sides of prosternal process parallel in female, not serrate and only slightly grooved (Fig. 145). First abdominal segment impunctate, obscurely foveolate, nonstriate; last segment obscurely punctate with shallow confluent foveae, its mid-ventral area flat with two groups of dense lateral hairs in male; female with large, deep, mid-ventral fovea with fewer hairs than in male. One large and one small spine on front tibia and single well developed spine on middle tibia in male; female tibiae without spines.

Aedeagus (Fig. 26) robust, truncate; ejaculatory guide as in Figure 55. Spermatheca (Fig. 82) with base of cornua slightly curved.

Types: Zimsen (1964) listed a single specimen of *gibbosus,* possibly the type, in the Fabrician collection at Kiel (now on loan to the Zoological Museum, Copenhagen). Dr. George W. Byers examined this specimen and a specimen in the Paris Museum, believed to be the type of *plicata.* Both were compared with a specimen in my collection and considered to be conspecific with it. On the basis of these comparisons, I consider *plicata* a junior synonym of *gibbosus.* The type locality for *gibbosus* was given as North America. The type locality for *plicata* is probably South Carolina, since it was collected by Bosc.

Discussion: This is the largest species of the genus in North America. It has been confused with several others, including the highly tuberculate *insularis* and *bimaculatus.* It also has a close affinity with *platani,* from which it can be distinguished by its larger size, the large, rounded elytral tubercles, regular and coarser striations on the pronotum, and especially



FIGS. **143-145.** *Neochlamisus gibbosus*. **143,** dorsal and lateral aspects; **144,** male prosternum; **145,** female prosternum.

the unequal tibial spines. Also, the truncate aedeagus is diagnostic for *gibbosus*. Another closely related species, *bebbianae,* can be distinguished from *gibbosus* by its smaller size, punctate pygidium, the presence of tibial spines in the females, and the pointed shape of the aedeagus. Variation creates problems in identification, since some individuals could be placed in any one of these four species, if only one or two characters are used. Each character must therefore be considered in combination with the others mentioned.

Parasites: This species is heavily parasitized by *Tetrastichus chlamytis* Ashmead and species of Ichneumonidae. Of 30 larvae collected at one locality in Texas, 25 were parasitized.

Plant records: Salix sp., *Rubus* sp., *Eubatus* spp. (series with larvae), *Quercus* sp., wheat and *Phleum pratense.*

Specimens examined (95 males and 186 females): (Map 6)

UNITED STATES: ALABAMA: Barbour Co., 18 June; Conecuh Co., 25 July; Houston Co., 16 May; Marshall Co., 25 May; Mobile Co., 20 May, 1-8 June, July; Shelby Co., 16 Apr., 17 July; Tallapoosa Co., Aug.; Tuscaloosa Co., 7 May. ARKANSAS: state record, 6 Oct. DISTRICT OF COLUMBIA: Brightwood, 20 July; Washington, 7 May, 2 July. FLORIDA: Alachua Co., 27 Feb., 14 Mar., 4-7 May, 12-24 June, 21 Oct.; Baker Co., 27 Apr., 26 May; Brevard Co., 10 Oct.; Clay Co., 12 June; Columbia Co., 14 June; Dade Co., 22 July; Duval Co., no date; Gadsden Co., 10 July; Hamilton Co., no date; Hernando Co., June; Jackson Co., 9 June; Nassau Co., 20 Aug.; Okaloosa Co., 30 July; Orange Co., Mar., 24 Apr.; Osceola Co., 7 Mar.; Pinellas Co., 14 Feb.; Polk Co., 6 May; Putnam Co., 24 May; Seminole Co., 7 May, 29 June; Volusia Co., 29 July; Walton Co., 8-10 July. GEORGIA: Chatham Co., June, 5 July; Clarke Co., 1 June; Cook Co., June; Dougherty Co., 23 July; Evans Co., 26 June; Fulton Co., 3 Mar.; Paulding Co., 22 Oct., Stewart Co., 18 Aug. ILLINOIS: Franklin Co., 26 May; Jackson Co., 27 May; Jefferson Co., 5 Aug.; Jo Daviess Co., no date; Marion Co., 31 May, 16 Aug.; Massac Co., 22 Apr.; Montgomery Co., 3 June; Perry Co., 6 Apr.; Pope Co., 13 May; Pulaski Co., 7 June; Saint Clair Co., 23 Apr.; Washington Co., 5 Apr., 10 Aug.; Wayne Co., 16 June. INDIANA: Boone Co., 2 May; Brown Co., 11 June; Owen Co., 25 May; Spencer Co., 11 Aug. LOUISIANA: DeSoto Par., 21 Apr.; Jefferson Par., 11 Apr., 17 June; Orleans Par., 28 Feb., 21 Apr.; St. Landry Par., 26 Apr.; St. Tammany Par., 4 June. MARYLAND: Prince Georges Co., 29 June. MICHIGAN: Montcalm Co., 14 May. MISSISSIPPI: Claiborne Co., 3 May; Granada Co., 11 June; Hancock Co., 21 May; Jackson Co., no date; Lowndes Co., 6 May; Wilkinson Co., 1 Aug. MISSOURI: Boone Co., 3 June, 14 July, 12 Aug.; Callaway Co., 10 July; Ozark Co., no date; St. Louis Co., 4 July. NEW MEXICO: Grant Co., 7 May. NORTH CAROLINA: Buncombe Co., 12 May, 20-23 June; Johnston Co., 22 May; Moore Co., 4 May, 14 June; New Hanover Co., 15 July; Wake Co., 2 June. OHIO: Highland Co., 8 June; Hocking Co., 20 June; Jackson Co., 6 Sept.; Scioto Co., 10 June; Washington Co., 15 June. OKLAHOMA: Muskogee Co., 24 May-6 June, 19 Sept. SOUTH CAROLINA: Aiken Co., no date; Beaufort Co., 15 July; Chester Co., 13 June; Dorchester Co., 17 Aug.; Horry Co., 11 Apr., 5 May; Orangeburg Co., 27 June. TEXAS: Anderson Co., 15 Apr.; Bastrop Co., 13 July; Bexar Co., 21 May; Blanco Co., no date; Bowie Co., 15 June; Brazos Co., 11 Apr.-11 May, 22-31 May, 13-14 June, 19 July, 29 Sept.; Cherokee Co., 2 Apr.; Colorado Co., 10 May; Comal Co., 8 July; Galveston Co., 26 May, 10-13 Aug.; Gillespie Co., 14 June; Gonzales Co., 19 Apr.; Lavaca Co., 27 May; Llano Co., 10 June; Kerr Co., 2 Apr., 18 Apr.; Matagorda Co., 20 July; Panola Co., 8 May; Sabine Co., 25 Mar.; Tyler Co., Sept.; Uvalde Co., 10 June; Val Verde Co., 7 June. VIRGINIA: Fairfax Co., 25 June, 8 July; Henrico Co., 26 June, 2 July; James City Co., 25 May.

MEXICO: No locality, no date.

Neochlamisus bimaculatus new species

Diagnosis: This species has small velvety spots on the elytra, similar to those found in the *velutinus* species group. It can also be identified by the lack of tibial spines in the females and two spines on each front tibia in males.

Description: Male holotype: 3.4 mm long; 2.6 mm wide. Color dark brown with metallic reflections, antennae yellowish brown.

Head faintly punctate, center of clypeus depressed and finely vermiculate, vertex finely striate. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum rough, faintly punctate, moderately and irregularly striate; tubercles faintly developed; posterolateral slopes with evenly spaced striae; posterior lobes transversely, finely striate and impunctate. Mesoscutellum granulate, posterior margin slightly depressed, posterolateral corners reflexed slightly. Elytra (Fig. 146) with large tubercles and carinae, moderately punctate; each discal velvety spot small, consisting of 4-6 deep punctures separated by sharp ridges; su-2 slightly crescent-shaped and carinate with su-1a; anterior 1/5 of elytral suture closed, posterior 4/5 serrate; anterior tubercles carinate or acute. Pygidium with smooth medial carina; large, confluent, shallow, circular foveae faintly vermiculate. Prosternum more than twice as long as wide. First ventral abdominal segment impunctate, granulate, with large obscure foveae; last abdominal segment faintly punctate, finely striate ventrally and granulate laterally. Two well developed spines on front tibia, single spine on middle tibia.

Aedeagus (Fig. 27) robust, truncate, with transparent apical edge; ejaculatory guide (Fig. 56) long and slim, length five times width.

Female allotype: 3.7 mm long; 2.8 mm wide. Color and sculpturing as in male. Apical spines of tibiae lacking; antennal segments as in male; mid-ventral fovea of last abdominal segment large and deep, lateral hairs long and more scattered than in males. Spermatheca (Fig. 83) conforms in general shape to those of other species in the genus.

Types: Male holotype, Baton Rouge (East Baton Rouge Par.), Louisiana, 27 Apr. 1934, F. E. Lyman (UK). Female allotype, Opelousas (St. Landry Par.), Louisiana, no date, G. R. Pilate (USNM). Sixteen paratypes: 1 ♂, Langdale, Chambers Co., Alabama, H. H. Smith (USNM); 1 ♂, Louisiana, A. Sallé (USNM); 1 ♀, Harahan (Jefferson Par.), Louisiana, 17 June 1944, F. G. Werner (MCZ); 2 ♀, Lafayette (Lafayette Par.), Louisiana, 19 Mar. 1908, on *Rubus,* R. A. Cushman (USNM); 2 ♀, Alexandria (Rapides Par.), Louisiana, 17 Mar. 1908, on *Rubus,* R. A. Cushman (USNM); 1 ♀, Mobile (Mobile Co.), Alabama, 2 June, 1906, H. P. Loding (UM); 1 ♀, Mobile Co., Alabama, June 1927, Darlington (MCZ); 2 ♀, Grenada Co., Mississippi, 21 April 1944, 11 June 1944, J. A. Wilcox (JAW); 2 ♀, Morton (Scott Co.), Mississippi, 10 Aug. 1959, S. D. and H. R. Burke (TAMU); 1 ♀, Montgomery Co., Mississippi, 7 May 1944, J. A. Wilcox (JAW); 1 ♀, 6 mi. N. Loachapoka, Lee Co., Alabama, 4 Apr. 1964, E. U. Balsbaugh, Jr., taken on *Rubus* (SDSU); 1 ♀, Ansby, Hancock Co., Mississippi, 8 Mar. 1966, H. R. Hepburn (JBK).

Discussion: This species is less variable than most of the others in the species group. It resembles in many respects *gibbosus* and *insularis,* except

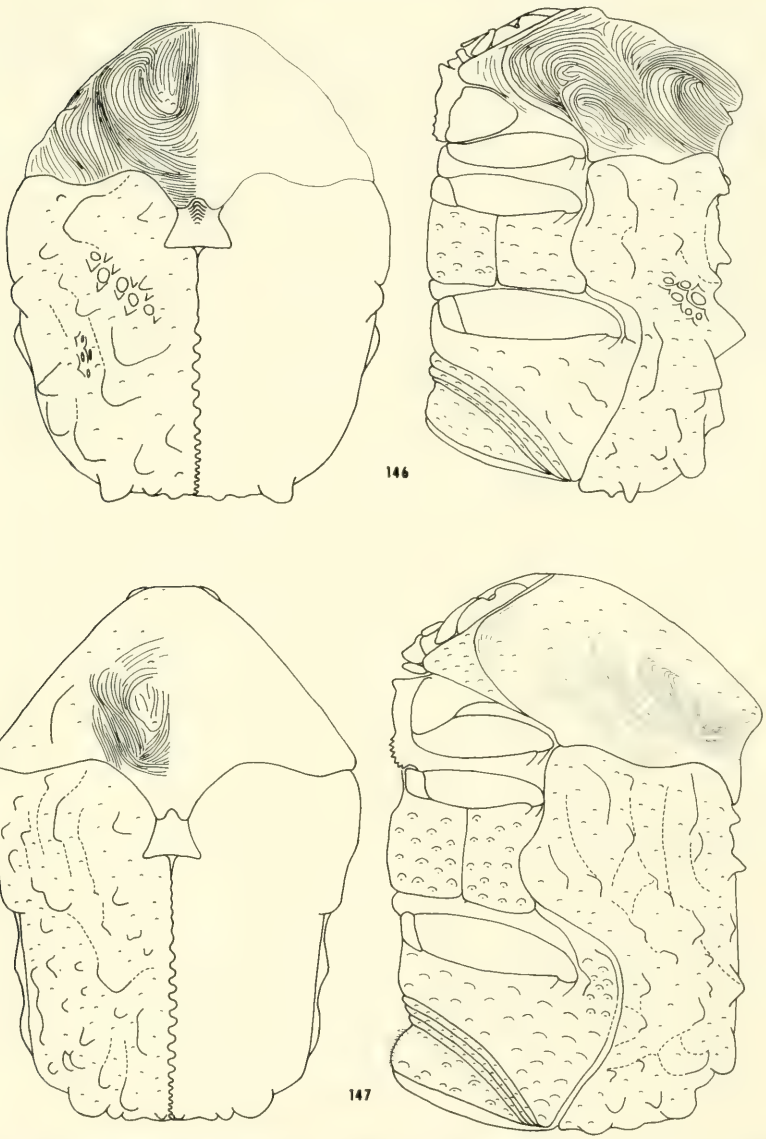


Fig. **146.** *Neochlamisus bimaculatus*, dorsal and lateral aspects. Fig. **147.** *Neochlamisus insularis*, dorsal and lateral aspects.

for the small velvety spots on each elytron. A few specimens of the latter two species have slight darkenings on the elytra that suggest faint velvety spots, but the deep punctures and sharp ridges are lacking. Some specimens have slightly convergent striations on the posterolateral slopes of the pro-

notum but they are never as rough and punctate as those found in the *velutinus* species group. The striate pronotum suggests a relationship to the *gibbosus* species group.

The finely vermiculate pygidium is similar to that of *eubati*, which also has faint indications of velvety spots. Vermiculation is so fine in many specimens that it is only clearly evident near the lateral and posterior borders of the pygidium.

Plant records: *Rubus* sp. (series), *Quercus* sp.

Specimens examined (12 males and 92 females): (Map 7)

UNITED STATES: ALABAMA: Chambers Co., no date; Clarke Co., no date; Lee Co., no date; Mobile Co., 2 June. ARKANSAS: White Co., 25 Apr. DISTRICT OF COLUMBIA: Brookland, 17 June. FLORIDA: Alachua Co., 12 Nov.; Escambia Co., 5 Aug.; Jackson Co., 23 Apr.; Leon Co., 1 Apr.; Nassau Co., 6 Aug. GEORGIA: Bibb Co., 4 May; Clarke Co., 15 May; Crawford Co., no date; Fulton Co., 6-18 May; Glynn Co., 21 July; Talbot Co., no date. LOUISIANA: East Baton Rouge Par., 27 Apr.; Jefferson Par., 17 June; Lafayette Par., 19 Mar.; Rapides Par., 17 Mar.; Sabine Par., 2 Apr.; St. Landry Par., no date. MARYLAND: Montgomery Co., 23 May. MISSISSIPPI: Grenada Co., 21 Apr., 11 June; Hancock Co., 8 Mar.; Montgomery Co., 7 May; Scott Co., 10 Aug. MISSOURI: St. Louis Co., no date; Vernon Co., 16 Apr. NORTH CAROLINA: Buncombe Co., no date; Johnston Co., 16-22 May; Wake Co., 29 May. SOUTH CAROLINA: Beaufort Co., 11-23 July; Charleston Co., 18 Aug.; Florence Co., 5 Mar.; Lee Co., 20 Apr.; Oconee Co., 31 May; Richland Co., 8 June. TENNESSEE: Shelby Co., 29 May. TEXAS: Anderson Co., 15 Apr.; Angelina Co., 6 Jan.; Bowie Co., 26-28 Mar.; El Paso Co., 7 June; Harris Co., 12 Apr.; Jasper Co., 21-25 Apr.; Panola Co., 8 May; Rusk Co., 8 June. VIRGINIA: Arlington Co., 18 May, 9 Sept.; Fairfax Co., 2 Aug.; Fauquier Co., 5 May; Hampton City, 18 Apr.; Montgomery Co., 23 May; Nansemond Co., 25 May; Northampton Co., 19-23 June; Nottoway Co., 7 May; Spotsylvania Co., May.

MEXICO: HIDALGO: 10 mi. NE Jacala, 1-2 Aug.

Neochlamisus insularis (Schaeffer)

Boloschesis insularis Schaeffer 1926:186.

Chlamisus jacobyi Blackwelder, 1946:648 (new synonymy; preoccupied by *Chlamisus jacobyi* (Achard), 1913).

Diagnosis: This species is easily recognized by the numerous deeply impressed punctures and many tubercles on the elytra, in addition to those normally found in related species. Each front tibia of males is armed with two subequal spines. The females usually have one spine, but there may be another partially developed.

Description: Male: 3.8-4.6 mm long; 2.8-3.6 mm wide. Female: 4.1-4.8 mm long; 3.1-3.7 mm wide. Color dark brownish to purplish or reddish bronze. Antenna yellowish brown; frons with large yellow spot in emargination of eye.

Head finely and faintly punctate, clypeus and vertex moderately punctate, center of clypeus and upper frons depressed, posterolateral corners not reflexed. Elytra (Fig. 147) moderately punctate, with large tubercles and carinae; many small tubercles present in addition to normal complement; general area of su-2a and ma-b represented by four well defined tubercles; punctures large and depressed; no discal velvety spots; su-2 round at apex,

broad at base; elytral suture closed and straight for anterior 1/5, remaining suture serrate, anterior tubercles rounded. Pygidium with smooth medial carina; foveae mostly confluent, granulate, slightly depressed, finely punctate except coarsely punctate at base; small shiny areas between punctures and foveae. Prosternum less than 1 1/2 times as long as wide, posterior process longitudinally grooved, explanate and finely serrate. First and last abdominal segments with large, granulate, punctate foveae, many foveae confluent and obscure; mid-ventral area of last segment flat, with scattered hairs in male; female with large, deep fovea, sides tumid, with long hairs. Two subequal, well developed spines on front tibia separated by a U-shaped space, single similar spine on middle tibia of male; female with single spine (rarely two) on front and middle tibiae.

Aedeagus (Fig. 28) robust, blunt pointed, with clear apical edge; ejaculatory guide as in Figure 57. Spermatheca as in Figure 84.

Type: Male holotype of *Boloschesis insularis* Schaeffer; Wilson City, Abaco, Bahamas, June, Coll. G. P. Engelhardt, USNM type 29465, labeled *Chlamys insularis* Schaeffer. The name *insularis* has been used for two other, different species of *Chlamys*. By placement of *insularis* Schaeffer in *Neochlamisus*, it is no longer a homonym. The new name, *Chlamisus jacobyi* Blackwelder (1946) proposed for *insularis* Schaeffer is no longer necessary and was itself a homonym when proposed.

Discussion: Most members are the most roughly sculptured of the North American species of *Neochlamisus*. This is because of the many tubercles on the elytra in addition to those normally present. The usual tubercles are small and divided so that the whole elytral surface is highly tuberculate. In most cases the foveae on the abdomen and pygidium are deep and convergent, imparting a rough appearance to these parts of the insect.

Many specimens from the southern states have been misidentified as *gibbosus*. In my paper on the genus *Exema* (Karren, 1966), it was noted that southern specimens of certain species were usually darker and rougher than those from the northern states. The rougher and more tuberculate sculpturing is accompanied by differences in the form of the genitalia and tibial spines. Some specimens of *insularis* are difficult to distinguish from the more tuberculate specimens of *gibbosus* except by these last named characters.

Predation: A series of 14 specimens was recovered by K. V. Krombein from nests of *Cerceris flavofaciata* excavated at Kill Devil Hills, Dare Co., North Carolina, 9 August 1958.

Plant records: Barletia cristata, Quercus sp. (series), *Myrica cerifera* (series).

Specimens examined (53 males and 270 females): (Map 8)

UNITED STATES: ALABAMA: Dallas Co., 8-9 Apr. FLORIDA: Alachua Co., 13 Feb., Mar.-26 June, 15 July, 26 Sept.-2 Oct., 19 Nov.; Brevard Co., 18 May, 8 Nov.; Broward Co.,

26 July; Charlotte Co., 16 May; Clay Co., 12 June; Collier Co., 18 Mar.; Dade Co., 3 Mar., 2-12 Apr., 12-26 May, 11 June, 25 June, 5 Nov.; DeSoto Co., 31 Mar., 30 Oct.; Duval Co., 9 May, 27 June, July, 3 Aug., 16 Aug.; Escambia Co., 4 Aug.; Hamilton Co., 6 June; Hendry Co., 11 Apr., 18-20 Apr.; Highlands Co., 4-6 Feb., 19 Apr.-1 June, 16-24 June, 13 July; Hillsborough Co., 3-5 Mar., 30 Mar.; Holmes Co., 12 June, 26 Aug.; Lake Co., 4 Mar.; Lee Co., 10 Mar., 28 Apr.; Levy Co., 14 Mar., 7 June-19 July; Liberty Co., 24 Apr.; Marion Co., 24 Oct.; Monroe Co., 28 Apr.; Nassau Co., 19 Aug., 31 Aug., 5 Oct.; Okaloosa Co., 15-16 Oct.; Orange Co., 15 Feb., 29-30 Apr., 10 Aug.; Osceola Co., 19 Feb.; Palm Beach Co., 21 Feb.; Pasco Co., 13 July; Pinellas Co., 21-30 Mar., 11 Apr., 28 Apr., 30 Oct.; Polk Co., 13 Feb., 10 Mar., 28 Mar., 5-8 May, 8-10 Nov.; Putnam Co., Apr.; Seminole Co., 28 Apr., 3-7 May, 1 June, 1 Sept.; Suwanee Co., 15 June; Volusia Co., 17 Mar., 15 Apr., 26 Apr., 16 May. GEORGIA: Chatham Co., 20-24 June; Fulton Co., 8 May; Glynn Co., 22 July; McIntosh Co., 26 Apr.; Richmond Co., 3 May; Ware Co., 26 June; Whitfield Co., 5 Oct. LOUISIANA: Jefferson Par., 7 June; St. Tammany Par., 2 June; Vernon Par., 25 Feb., 14 Mar. MISSISSIPPI: Harrison Co., June; Jackson Co., 10 July. NORTH CAROLINA: Jones Co., 15 Sept. SOUTH CAROLINA: Bamberg Co., 15 Aug.; Beaufort Co., 11-23 July. TEXAS: Blanco Co., no date; Uvalde Co., 25 Aug.; Walker Co., 1 May, 9 July; Webb Co., no date.

Neochlamisus platani (Brown)

Chlamisus platani Brown, 1952:338-339.

Diagnosis: The bright yellowish bronze color when present is the most obvious and easily recognized characteristic of this species. In addition, it differs from related species by the finely striate pronotum with striae usually convergent on posterolateral slopes, foveolate pygidium and ventral abdominal segments, and two equal spines on each anterior tibia of the male.

Description: Male: 3.2-4.1 mm long; 2.4-2.9 mm wide. Female: 3.7-4.6 mm long; 2.8-3.3 mm wide. Color bright reddish to yellowish bronze, occasionally dark brownish bronze; antennae light brown.

Head rough, clypeus and lower frons vermiculate, vertex striopunctate between eyes, central area of upper frons depressed. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular, segments 4-6 slightly smaller in female than in male. Pronotum rough, finely and irregularly striate, mp and la tubercles slightly developed; gibbosity deeply divided, posterolateral slopes striate, striae converging on area at middle of base of posterolateral slopes; posterior lobes finely and transversely striate. Mesoscutellum granulate, with anterior medial carina, posterior margin slightly depressed, posterolateral corners reflexed. Elytra (Fig. 148) with large tubercles and carinae, moderately punctate, punctures depressed, anterior tubercles rounded or sharply carinate; elytral suture closed anteriorly, posterior 7/8 serrate. Pygidium with smooth medial carina, many deep to shallow foveae, foveae usually shallow and confluent. Prosternum nearly 1 1/2 times as long as wide, posterior process slightly grooved, explanate and serrate. First abdominal segment with large, granulate, shallow foveae, last segment with small mid-ventral foveae in male; mid-ventral fovea of female large and deep with long hairs on anterolateral border. Two well

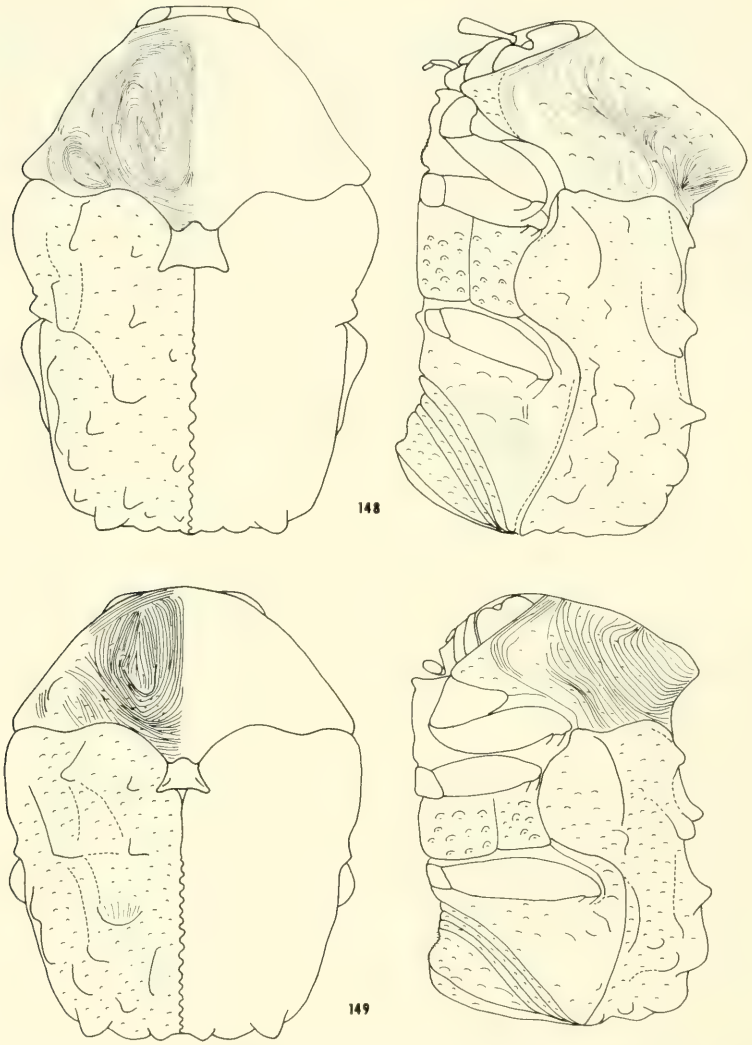


Fig. **148.** *Neochlamisus platani,* dorsal and lateral aspects. Fig. **149.** *Neochlamisus bebbianae,* dorsal and lateral aspects.

developed spines on front tibia of male; middle tibia of male and front and middle tibiae of female with similar single spine.

Aedeagus (Fig. 29) acute at apex, robust; ejaculatory guide (Fig. 58) long and slim, more than five times as long as wide, sheath hinged near middle of asymmetrical paired structures. Spermatheca (Fig. 85) nearly U-shaped with slight apical swelling.

Types: The male holotype and female allotype are both in the personal

collection of John A. Wilcox, Albany, New York. The above description was taken from these specimens. They bear the following label data: Lorain Co., Ohio, 7 Sept. 1947, *Platanus*, J. A. Wilcox, Collr. Eleven paratypes, from the type locality, collected on various dates were also examined.

Discussion: Most specimens are brightly colored, but samples from apparently the same population may contain specimens of the dark form. This color variation is not correlated with locality, host plant or season.

Considerable variation is also found in the sculpturing of this species. Generally the posterolateral slopes of the pronotum are diagnostic and have fine convergent striae, but in some specimens the striation is more coarse and follows the contours of the gibbosity rather than converging on the base. Others have only a few convergent and many sinuous striae. In these specimens the other diagnostic characters of the species must be used in order to make a correct identification.

The host specificity originally described for the species does not exist. At least three samples have been taken from hosts other than *Platanus* in each of which larval or adult feeding has been observed. These specimens vary but are as similar to the type of *platani* as are the paratypes.

Females of this species exhibit considerable variation in the development of the apical spines of the front and middle tibiae. This variation appears to be geographical in that many of the eastern examples have a small second spine or a raised edge on the front tibiae. A short series of females from Estero, Florida, has two equal tibial spines similar to those found in males from elsewhere.

The pronotum may be moderately and irregularly striate in all specimens in certain samples. Host data are lacking for all such specimens, but I have placed them in *platani* because of their agreement in other diagnostic characters, and because they come from within the geographical range of the species. They will most likely be confused with *bebbianae*, except for their bright reddish bronze color, moderately punctate elytra and many carinate tubercles.

Plant records: Platanus occidentalis (series with larvae), *Corylus americana* (series), *Betula nigra* (series), *Ulmus* sp., *Trifolium pratense*.

Specimens examined (33 males and 148 females): (Map 9)

UNITED STATES: ARKANSAS: Pulaski Co., 28 Apr.; Washington Co., 6-27 July. COLORADO: El Paso Co., no date; Logan Co., 22 May. DISTRICT OF COLUMBIA: Washington, 14 June, 1-13 Aug. FLORIDA: Holmes Co., 6-12 May; Polk Co., 20 Mar.; Volusia Co., no date. GEORGIA: Clarke Co., 21 Oct.; Glynn Co., 22 July; Whitfield Co., 25 May, 24 July. ILLINOIS: Alexander Co., 2 May; Champaign Co., 9 May; Cook Co., 13 May; Fayette Co., 19 Apr.; Gallatin Co., 27 May; Jefferson Co., 5 Aug.; Johnson Co., 4-7 June, 16 July; Logan Co., 11 June; McHenry Co., no date; Paulding Co., 6 Apr.; Pope Co., 10 May, 17 Oct.; Vermilion Co., 6 Apr.; Washington Co., 24 May. INDIANA: Harrison Co., 27 June, 28 Aug. IOWA: state record, 6 Sept. KANSAS: Douglas Co., 30 Apr.-18 June, 25 Sept., 15 Oct.; Reno Co., May; Shawnee Co., 24 Aug.; Wilson Co., 7 May. KENTUCKY: Butler Co., 16 June. LOUISIANA: Claiborne Par., 14 July. MARYLAND: Montgomery Co., 6 Mar.,

26 Apr., 23 May-23 June, 4 July, 25 July. MASSACHUSETTS: Hampden Co., no date. MISSISSIPPI: Forrest Co., 24 Apr.; Grenada Co., 18 May. MISSOURI: Boone Co., 19 May, 10 June, 12 Aug.; Jackson Co., 5 July. NEW JERSEY: Cape May Co., 13 July. NEW YORK: Suffolk Co., 14 May. NORTH CAROLINA: Moore Co., no date. OHIO: Delaware Co., 21 June, 2 July; Franklin Co., 9 June; Hocking Co., 8 May, 20 May-6 June; Lorain Co., 27-29 July, 17-24 Aug., 7 Sept. OKLAHOMA: Murray Co., 14 May. PENNSYLVANIA: Montgomery Co., 4 May. SOUTH CAROLINA: Beaufort Co., 11 Oct. TENNESSEE: Lake Co., 2 June; Montgomery Co., 16 May. TEXAS: Blanco Co., no date; Cherokee Co., 2 Apr.; Cottle Co., 15 Mar.; Crosby Co., 2-17 Mar.; Gillespie Co., 5 Apr.; Harris Co., 3 Aug.; Jeff Davis Co., 25 June; Kerr Co., 23 Apr.; Leon Co., 23 Aug.; Rusk Co., 8 June; Travis Co., 13 Feb. VIRGINIA: Fairfax Co., 27 June, 8 Aug.; Loudon Co., 8 Oct.; Montgomery Co., 5 May, 5 Oct., 19 Oct. WEST VIRGINIA: Greenbrier Co., 18 June.

Neochlamisus bebbianae (Brown)

Arthrochlamys bebbianae Brown, 1943:128-130.
Arthrochlamys alni Brown, 1943:128 (new synonymy).
Arthrochlamys tecta Brown, 1946:48-49 (new synonymy).
Chlamisus alni (Brown); Brown, 1961:971.

Diagnosis: One can identify this species by its moderately to coarsely punctate pygidium, obscure foveae on the abdominal segments, moderately punctate elytra, and irregular and moderately striate posterolateral slopes of the pronotum.

Description: Male: 3.2-4.1 mm long; 2.6-3.0 mm wide. Female: 3.8-4.1 mm long; 2.6-3.1 mm wide. Color dark brownish bronze, occasionally bright reddish bronze; antennae yellowish to light brown, gradually becoming darker toward apex.

Head moderately punctate, clypeus and genae vermiculate, vertex faintly striopunctate, upper frons with a medial depression. Antennal segment 4 subcylindrical, 5 subtriangular, 6 subrectangular, 7-10 rectangular. Pronotum rough, moderately and irregularly striate, mp tubercle faintly developed; gibbosity deeply divided, posterolateral slopes irregularly striate, some but never all striae convergent ventrally; posterior lobes finely and transversely striate, impunctate. Mesoscutellum granulate, posterior margin flat to slightly depressed, posterolateral corners reflexed slightly. Elytra (Fig. 149) with large tubercles and carinae, moderately punctate; anterior elytral suture closed, posterior 4/5 serrate; anterior tubercles round, acute or carinate. Pygidium moderately to coarsely punctate, with irregular medial carina, depressed areas confluent. Prosternum less than 1 1/2 times as long as broad, posterior process faintly grooved and obscurely serrate. Last abdominal segment foveolate, mid-ventral area flat with numerous long hairs in male; female with large mid-ventral fovea with long anterolateral hairs; first segment obscurely foveolate. Two well developed spines on front tibia, single spine on middle tibia in male; female with single spines on front and middle tibiae.

Aedeagus (Fig. 30) acute with transparent apical area; ejaculatory guide (Fig. 59) long and narrow. Spermatheca as in Figure 86.

Types: Arthrochlamys bebbianae: male holotype, Arnprior, Ontario, reared from larva taken on *Salix bebbiana* in August 1942, W. J. Brown, no. 5405 in the Canadian National Collection. *Arthrochlamys alni:* female holotype, Norway Bay, Quebec, on *Alnus incana americana,* 30 August 1942, W. J. Brown, no. 5404 in the Canadian National Collection. *Arthrochlamys tecta:* male holotype, Walsingham, Ontario, 29 May 1944, on *Corylus americana,* W. J. Brown, no. 5614 in the Canadian National Collection. Paratypes have been examined from each of the type series.

Discussion: Brown first segregated the species in the *gibbosus* complex in 1943. At that time it appeared that many, if not all, of the species were host specific. Brown studied principally the Canadian species, more specifically those of eastern Canada. On the basis of samples collected from one host plant, Brown described several "sibling species" in this complex. He admitted that there was no morphological means of differentiating some of these species. Others were so similar that only specimens in a series associated with a particular host could be correctly identified.

By studying a large number of specimens from eastern United States, including many series associated with host plants, I have found that the species of this complex are less host specific than was at first suspected. Some of the forms recognized by Brown as sibling species are only variants of more widespread species. Further study of this group by Brown (1952) suggested that some species may prefer a particular host, but will move to other acceptable plants when the preferred host becomes unavailable. It also seems that when the usual food plant is not present in a given locality, different plants become the preferred hosts.

I have accordingly synonymized *tecta* and *alni* under *bebbianae.* This species has a wide distribution with considerable morphological variation, but no more than the other North American species of this genus. Specimens are generally of medium size, dark in color and moderately tuberculate, striate and punctate. The posterolateral slopes of the pronotum are usually somewhat irregularly striate, but in some specimens the striations are not broken or convergent. In a few others the striations are irregularly convergent. Individual tubercules and carinae of the elytra vary in every species so that one must use these characters in combination with others to identify species.

There is little variation in the form of the apical tibial spines. They are sometimes difficult to see because of the position of the legs and may be concealed by apical hairs.

Predation: A series of 55 specimens was recovered by J. C. Bridwell at Vienna, Virginia, from nests of *Cerceris fumipennis* (Scullen, 1965).

Plant records: Salix bebbiana (series with larvae), *S. humilis* (series with larvae), *Corylus americana* (series), *Alnus rugosa* (series with larvae), *A. serrulata* (series, literature record), *Ulmus* sp. (series), *Acer rubrum* (series with larvae), *Verbascum* sp., *Iris versicolor, Juglans rupestris* (series), *J. nigra, J. cinerea, Quercus* sp. (series), *Hamamelis virginiana, Betula nigra* (series with larvae).

Specimens examined (148 males and 905 females): (Map 10)

UNITED STATES: ALABAMA: Baldwin Co., 15 May; Barbour Co., 24 Feb.; Hale Co., 13 May; Mobile Co., 12 Apr., 17 June, July. ARKANSAS: Boone Co., no date. ARIZONA: Pinal Co., no date; Santa Cruz Co., no date. CONNECTICUT: Fairfield Co., June, 5-18 July, 25 Aug.; Litchfield Co., 30-31 May, 23 June; New Haven Co., 14-20 June; New London Co., 23 May, 4 July; Windham Co., 25 June. DISTRICT OF COLUMBIA: Washington, May, 5 June, 5 July, 31 July. FLORIDA: Bay Co., 20 May; Dade Co., 11 May; Highlands Co., 5 May, 16 June; Jackson Co., 7 Mar.; Lee Co., 6-12 May; Liberty Co., 16 Apr.; Manatee Co., 25 Mar.; Nassau Co., 19 Aug.; Okaloosa Co., 9 July; Suwannee Co., 4 Aug. GEORGIA: Baldwin Co., 6 May; Bibb Co., 13 May; Chatham Co., 2-3 July; Clarke Co., 24 Apr.-2 May, 18 May; Crawford Co., 12 May; McIntosh Co., 28 Apr.; Meriwether Co., 9 May; Pike Co., no date; Rabun Co., 10 May. ILLINOIS: Calhoun Co., 10 Oct.; Cook Co., 21-28 June, 5 Sept.; Lake Co., 24 Aug.; McHenry Co., no date; Pope Co., 30 Apr.; Woodford Co., 6 June. INDIANA: Lake Co., 18 June. IOWA: Boone Co., 2 Oct.; Pottawatomie Co., 26 June. KANSAS: Douglas Co., 24 Sept.; Leavenworth Co., 1 July; Montgomery Co., 26 Aug.; Riley Co., May; Shawnee Co., no date. KENTUCKY: state record, no date. LOUISIANA: Calcasieu Par., 10 Aug.; St. Tammany Par., 29 Mar.; Vernon Par., 25 Feb. MAINE: Penobscot Co., 24 May; Piscataquis Co., 29 June. MARYLAND: Baltimore Co., 6 June, 11 July; Montgomery Co., 12 Apr., 5 May, 17 May, 8-13 June, 5-10 July, 5 Aug., 17 Aug., 30 Aug.; Prince Georges Co., 17 May, 4 June, 4-5 July, 17 Sept.; St. Marys Co., 12 July, 3 Sept. MASSACHUSETTS: Barnstable Co., 4 July, 27 Aug; Bristol Co., 19 June, 6 Sept., 22 Sept.; Essex Co., 26 May, 12 June; Hampden Co., 10 June, 28 June, 7 July, 16 Aug., 20-22 Sept.; Hampshire Co., 17 Aug.; Middlesex Co., 21 May-10 June, 8 July, 22 July, 10-19 Aug., 30 Aug.; 7 Sept.-22 Oct.; Norfolk Co., 9 June; Worcester Co., 19 May, 31 May, 21 Aug. MICHIGAN: Cheboygan Co., 26 June, 8 July, 1 Aug.; Chippewa Co., 2 July; Grand Traverse Co., 27 May; Livingston Co., 12 June, 12 July; Osceola Co., 24 May; Washtenaw Co., 8 May; Wayne Co., 5 Sept., 5 Oct. MINNESOTA: Anoka Co., 17 Sept.; Hubbard Co., 27 May, 4 June, 15-28 June, 11 Aug.; Mille Lacs Co., 3 June; Olmstead Co., 4 July, Polk Co., 11 Aug.; Red Lake Co., 10 June; Stone Co., 15 Aug. MISSOURI: Boone Co., 20-23 Apr., 16 May; Howell Co., 8 June; Jackson Co., 25 May; Lincoln Co., 26 Aug.; St. Louis Co., 7 June; Vernon Co., 4 Oct. NEBRASKA: Cherry Co., 10 June; Douglas Co., 30 June; Holt Co., 9 Sept.; Keyapaha Co., 10 June; Nance Co., 1 July; Thomas Co., 4-5 July. NEW HAMPSHIRE: Carroll Co., 24 June; Rockingham Co., 7 May. NEW JERSEY: Atlantic Co., 5 June, 10-17 July; Bergen Co., 15 May; Burlington Co., 25 May, 4 July; Camden Co., 23 May-13 June; Cape May Co., 31 May, 13 July; Essex Co., 26 May, 8 June; Mercer Co., 23 Apr.; Morris Co., 26 May; Ocean Co., 13 May, 30 May, 24-26 Sept.; Union Co., 9 Sept. NEW YORK: Albany Co., 11 May, 24 May, 11 June, 25 Aug.; Cortland Co., 7 June; Dutchess Co., 2-11 June, 10 Aug., 30 Aug.; Erie Co., 28 June; Herkimer Co., 22 May; Monroe Co., Oct.; Orleans Co., 15 June; Putnam Co., 4 May; Queens Co., June; Richmond Co., 24 June-2 July; Rockland Co., 28 June; St. Lawrence Co., 30 June; Suffolk Co., 28 May; 11-17 June, Aug.; Sullivan Co., 3 Sept.; Tioga Co., 24 Apr.; Tompkins Co., 14-22 May, 4 June; Westchester Co., 17 Mar., 26 May, 2 June, 30 Oct.; Wyoming Co., 2 June. NORTH CAROLINA: Buncombe Co., no date; McDowell Co., 27 May; Moore Co., 4-10 May; New Hanover Co., 26 July. OHIO: Champaign Co., 22 May, 8 Oct.; Cuyahoga Co., 19 May; Delaware Co., 2 July; Erie Co., 1 Sept.; Fairfield Co., 29 June, 15 Aug.; Fulton Co., 2 Sept.; Greene Co., 30 May-5 June, 13 Sept.; Hocking Co., 13 May-2 June, 20 June, 2-10 July, 15-24 Sept.; Medina Co., 11 June, 28 Aug.; Ross Co., 21 Sept.; Scioto Co., 30 May-17 June; Wayne Co., 11 May. OKLAHOMA: Comanche Co., 30 May. PENNSYLVANIA: Allegheny Co., 4 July; Dauphin Co., 25-30 May, 4-5 July, 2 Sept.; Delaware Co., June; Fayette Co., 23 June; McKean Co., 16 May, 9 June, 21-30 June; Monroe Co., no date; Northampton Co., 7-14 June, 28 June, 11 July; Philadelphia Co., 15 June, 29 July; Pike Co., 9 June; Wyoming Co., 8 May. SOUTH CAROLINA: Charleston Co., 2 July; Pickens Co., 6 July. SOUTH DAKOTA: Bennett Co., 11-12 Sept.; Corson Co., 8 Sept.; Yankton Co., 15-20 June. TENNESSEE: Campbell Co., 27 Aug.; Davidson Co., 23 June; Sevier Co., 14 June. TEXAS: Aransas Co., 31 Mar.; Brazos Co., 4 Mar., 19-24 Apr., 3 May, 15 May, 9 Oct.; Cameron Co., 30 Mar., 22-26 Apr., 25 June, 8 Dec.; Colorado Co., 11-20 Apr.; Cottle Co., 15 Mar.; Dallas Co., no date; Eastland Co., 4 June; Gillespie Co., 7 May, 6 June, 23 June; Harris Co., 4 Aug.; Hidalgo Co., 24 Mar., 10 May; Houston Co., 22 Apr.; Jeff Davis Co., 19 June, 4 July; Kendall Co., 11 July; Kerr Co., 31 Mar.-14 Apr., 22-27 Apr.; Leon Co., 23 Aug.; Montague Co., 26 Apr.-2 May; Montgomery Co.,

23 Aug.; Pecos Co., 24 Apr.; Real Co., 29 July; Travis Co., 28 June; Uvalde Co., 23 May, 13-15 June, 25 Aug.; Val Verde Co., 9 Mar., 3 May. VERMONT: Orange Co., 23-27 May; Windham Co., spring. VIRGINIA: Arlington Co., 1-19 May, 8 Aug., 20-30 Sept.; Caroline Co., 30 Sept., 12 Oct.; Fairfax Co., 30 Apr.-5 May, 18 May, 22 June; Prince William Co., 28 Sept.; Spotsylvania Co., 21 Mar., May. WISCONSIN: Polk Co., 13 Aug.; Shawano Co., 13-16 Sept.; Washburn Co., 22 June; Wood Co., 13 Sept.

CANADA: NOVA SCOTIA: Hants Co., no date. ONTARIO: Addington and Lennox Co., 16 June; Carleton Co., 3-13 May, 30 May, 19 Aug., 31 Aug., 3 Sept., 14 Sept.; Oxford Co., 30 May; Parry Sound Co., 31 July; Prince Edward Co., 19 June; Renfrew Co., 2 May, 24 May, 15 Aug., 7-8 Sept.; Russell Co., 20 Aug., 5 Sept. QUEBEC: Pontiac Dist., 24 May, 30 Aug., 3-10 Sept.

Neochlamisus eubati (Brown)

Arthrochlamys eubati Brown, 1943:126-127.
Arthrochlamys coryli Brown, 1946:48 (new synonymy).
Chlamisus eubati (Brown); Wilcox, 1954:396.

Diagnosis: This species is recognized by the deeply divided pronotal gibbosity, vermiculate pygidium, vermiculate and striate last abdominal segment and the two equal spines on the front tibia of the males.

Description: Male: 3.3-3.7 mm long; 2.5-2.7 mm wide. Female: 3.7-4.5 mm long; 2.8-3.4 mm wide. Color black to dark reddish brown with metallic reflections; antennae yellowish brown at base, becoming darker brown at apex, mandibles light brown to black.

Head moderately punctate, center of clypeus depressed and vermiculate, vertex coarsely punctate. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum moderately striate, impunctate, tubercles faintly developed; posterolateral slopes regularly striate, gibbosity deeply divided; posterior lobes transversely and finely striate, impunctate. Mesoscutellum granulate, posterior margin depressed, posterolateral corners reflexed slightly. Elytra (Fig. 150) with large tubercles and carinae, moderately punctate; punctures with radiating striae; often faint discal velvety spots consisting of 3-4 deep punctures separated by sharp ridges; su-2 broad with low-angled anterior slope; anterior part of elytral suture closed, posterior 4/5 serrate, anterior tubercles rounded. Pygidium vermiculate, moderately punctate, foveae shallow, confluent and obscure. Prosternum more than 1 1/2 times as long as wide. First abdominal segment obscurely foveolate and striate; last segment striate and vermiculate, mid-ventral area with two groups of lateral hairs in male, female mid-ventral fovea large but shallow, with hairs more scattered than in male. Two well developed spines on anterior tibia, single similar spine on middle tibia of male; female without tibial spines.

Aedeagus (Fig. 31) with bluntly pointed, scarcely deflexed apex; ejaculatory guide (Fig. 60) long and slim, length five times width. Spermatheca as in Figure 87.

Types: Arthrochlamys eubati: male holotype, Kirk's Ferry, Quebec, on *Rubus (Eubatus)* sp., 27 May 1942, W. J. Brown, no. 5403 in the Canadian National Collection. *Arthrochlamys*

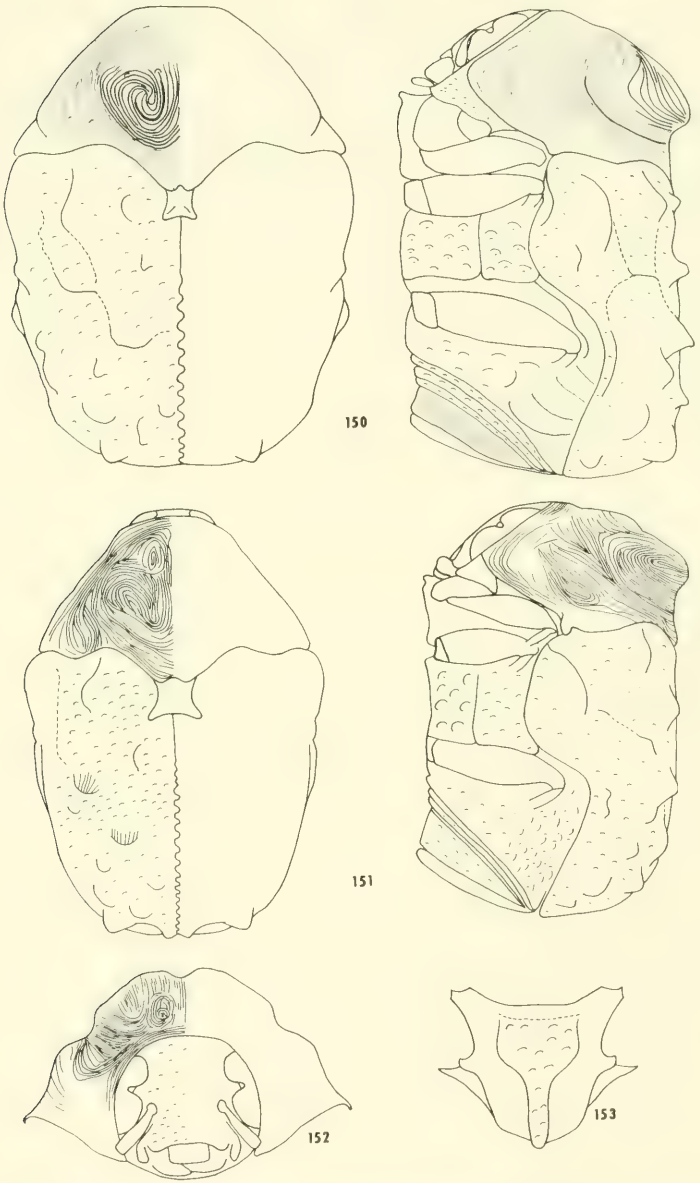


Fig. **150.** *Neochlamisus cubati,* dorsal and lateral aspects. Figs. **151-153.** *Neochlamisus comptoniae.* **151,** dorsal and lateral aspects; **152,** cephalic aspect; **153,** prosternum.

coryli: female holotype, Walsingham, Ontario, on *Corylus americana,* 30 May 1944, no. 5613 in the Canadian National Collection. I have examined paratypes from both type series.

Discussion: The type series (all females) of *coryli* was collected on hazel. Brown considered *coryli* distinct from *eubati* because of different host plants, sex ratios, and because of slight morphological distinctions. I can find no consistent diversity between these two named forms, either in the two series of paratypes or in numerous other examples. Differences pointed out in the original description are well within the range of variation of *eubati,* especially when one considers the species from its entire geographic range.

Since several species in this group have been taken on a variety of host plants and exhibit widely differing sex ratios from one collection to another, it seems unlikely that the host plant and sex ratio ascribed to *coryli* are valid specific characters. There is less variation in this species than in several others of the *gibbosus* group. Some is found in the striate and vermiculate surface of the last abdominal segment. In a few specimens the lateral areas of the segments are granulate and faintly punctate. There is sometimes a little irregularity in the striation of the posterolateral slopes of the pronotum.

The mid-ventral fovea of the last abdominal segment of the female is not as deep as it is in most other species of the *gibbosus* group.

Plant records: Geum album (series), *Aster* sp., *Rubus frondosus, R. (Eubatus)* spp. (series with larvae), *Alnus* sp. (series), *Phleum pratense* (series with larvae), *Barbarea vulgaris* (series), *Potentilla fruticosa* (series, literature record), *Ulmus* sp., *Corylus americana, Solidago* sp.

Specimens examined (66 males and 429 females): (Map 11)

UNITED STATES: ARKANSAS: White Co., 25 Apr. ARIZONA: Navajo Co., 20 July. COLORADO: Boulder Co., 9 Apr., 16 June, 8-10 Aug. CONNECTICUT: Fairfield Co., 9 May, 30 May-10 June; Litchfield Co., 14 May, 23 June; New Haven Co., 9-22 June; New London Co., 5-9 Aug. DISTRICT OF COLUMBIA: Washington, 23-25 July. FLORIDA: Pinellas Co., 27 Feb. GEORGIA: Murray Co., 9 Aug. ILLINOIS: Alexander Co., 7 Oct.; Clay Co., 31 May; Crawford Co., 8 June; Jackson Co., 26 June; Johnson Co., 23 May; Mason Co., 1 Aug.; Platt Co., 24 May. INDIANA: Brown Co., 2 Oct.; Crawford Co., 1 June; Lake Co., 24 May, 22 Sept.; Marion Co., 17 May; Perry Co., 16-23 May; Spencer Co., 24-25 May; Starke Co., 18 June. IOWA: Dickinson Co., 1 July, 22 Aug.; Henry Co., 13 June. KANSAS: Shawnee Co., no date. KENTUCKY: Bullitt Co., 9 May. LOUISIANA: state record, no date. MARYLAND: Baltimore Co., Apr., 6 June; Frederick Co., 18 June; Montgomery Co., 30 Apr., 10-18 May, 8-15 June; Prince Georges Co., 6 Mar., 14-15 May, 9 Aug., 16 Sept.; Washington Co., 8 June. MASSACHUSETTS: Bristol Co., 19 May; Essex Co., 3 June; Hampshire Co., June; Middlesex Co., 17-27 May, 23-27 June, 1 Aug., 22-28 Aug., 28 Sept.; Norfolk Co., 17 June; Suffolk Co., 26 June, 21-25 July. MICHIGAN: Allegan Co., 11 Sept.; Berrien Co., Aug.; Oscoda Co., 19 Aug. MINNESOTA: Anoka Co., 3 June; Big Stone Co., no date; Hubbard Co., 17 June; Olmstead Co., 13 June, Sept.; Ottertail Co., no date; Red Lake Co., 3 Aug.; St. Louis Co., 1 June, 5 Sept. MISSOURI: Boone Co., 25 May; Camden Co., May; Iron Co., 19 May; Jefferson Co., no date; Pike Co., 20 Apr., 3 Oct.; St. Louis Co., 5 Sept.; Stoddard Co., 17 June. MONTANA: Carter Co., 5 Sept.; Rosebud Co., 20 June. NEBRASKA: Cuming Co., June; Thomas Co., 9 June, 4 July, 4 Aug. NEW HAMPSHIRE: Rockingham Co., 6 June. NEW JERSEY: Bergen Co., 25 Apr., 16 June; Burlington Co., 4 June; Camden Co., 6 Mar., 27-30 May; Essex Co., 30 May; Hudson Co., 21 Apr.; Mercer Co., 1 Aug.; Middlesex Co., 22 Apr.; Morris Co., 15 Apr., 29 Apr., 13-29 June; Ocean Co., 9 May; Passaic Co., 25 July, 7 Aug.; Sussex Co., 24 May, 6 June; Union Co., 3 June; Warren Co.,

21 May. NEW YORK: Albany Co., 15-31 May, 3-11 June; Dutchess Co., 27 May, 16 June; Kings Co., 27 May, 18 July; Monroe Co., 30 May; Nassau Co., 6 Apr., 24 June; New York Co., 11 Apr., 24 May; Niagara Co., 4 Aug.; Orange Co., 26 May; Orleans Co., 15 June; Rensselaer Co., 17 Aug.; Rockland Co., 27 May; Saratoga Co., 2 June; Suffolk Co., 14 May, 23 July; Tompkins Co., 17-21 May, 4-8 June; Ulster Co., 18 June; Westchester Co., Sept. NORTH CAROLINA: Buncombe Co., 12 May, 23 May; Haywood Co., May-June; Macon Co., no date. NORTH DAKOTA: Burleigh Co., 19 Sept.; Cass Co., 16 June; Traill Co., 4 Aug. OHIO: Clinton Co., 12 May, 29 May, 21 June; Greene Co., 2 June, 23 June; Hocking Co., 10-23 May, 2 June, 14-20 June, 2 July, 5 Sept.; Jackson Co., 19 Aug.; Lorain Co., 6 June; Perry Co., 9 June; Scioto Co., 5 May, 9 June; Summit Co., 15-16 June. PENNSYLVANIA: Allegheny Co., May; Bucks Co., no date; Centre Co., 15 June; Delaware Co., 7 May, 27 May, 2-16 June, 30 Aug.; Franklin Co., 13 June; Montgomery Co., 13-17 May, 29 May; Northampton Co., 31 May-7 June; York Co., 15 June. SOUTH DAKOTA: Brookings Co., no date; Brule Co., 5 June; Custer Co., 19 June; Fall River Co., 11 Sept.; Jackson Co., 9 June; Lawrence Co., 26 July, 10-11 Sept.; Marshall Co., 18 Sept. UTAH: Uintah Co., 13 June. VIRGINIA: Alexandria Co., 4 May, 18 June, July-Aug.; Arlington Co., 9-18 May, 1 June, 28 June, 8 July; Fairfax Co., 17 Apr., 16 June, 14 Aug., 27 Aug. WEST VIRGINIA: Greenbrier Co., no date.

CANADA: ALBERTA: Edmonton, 5-9 May, 1 Nov. ONTARIO: Carleton Co., 9 May, 7 June, 22-30 July, Aug.-Sept.; Renfrew Co., 26 Aug. QUEBEC: Wright Dist., 27 May, 18 Sept.

MEXICO: No locality, no date.

Neochlamisus fragariae (Brown)

Chlamisus fragariae Brown, 1952:337-338.

Diagnosis: The faintly divided pronotal gibbosity, vermiculate pygidium and single tibial spines in the males together distinguish this species.

Description: Male: 3.2-3.5 mm long; 2.3-2.5 mm wide. Female: 3.5-4.2 mm long; 2.6-2.9 mm wide. Color black to dark reddish bronze, antennae yellowish brown at base becoming darker brown at apex, mandibles dark brown.

Head moderately punctate, center of clypeus slightly depressed, lower frons and clypeus vermiculate, vertex faintly punctate and striate. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum moderately striate, impunctate, tubercles faintly developed; posterolateral slopes regularly striate, gibbosity faintly divided; posterior lobes transversely and finely striate, impunctate. Mesoscutellum granulate, posterior margin slightly depressed, posterolateral corners reflexed slightly. Elytra with moderate tubercles and few carinae, finely punctate, punctures with radiating striae; discal velvety spots faint, consisting of several deep punctures; su-2 broad, with slowly rising anterior slope; anterior elytral suture closed, posterior 4/5 serrate; anterior tubercles small and rounded. Pygidium vermiculate, moderately to coarsely punctate, most of circular areas confluent and obscure. Prosternum about twice as long as wide. First abdominal segment obscurely foveolate and striate; last segment striate and vermiculate, mid-ventral area with two groups of lateral hairs; female mid-ventral fovea shallow and large, with hairs more scattered than in male. Single well developed spine on anterior and middle tibiae of male; female without tibial spines.

Aedeagus (Fig. 32) as in *eubati;* ejaculatory guide (Fig. 61) long and slim. Spermatheca as in Figure 88.

Type: Male holotype, Hatfield Point (Kings Co.), New Brunswick, 17 Sept. 1951, G. T. Morgan, on *Fragaria ananassa;* no. 5984 in the Canadian National Collection. Allotype, same data. I have examined one male and two female paratypes.

Discussion: A very short series was available for study so that information about variability is limited. This species is very similar to *eubati,* except for the single spine on the front tibia of the males, faintly divided pronotal gibbosity and other slight morphological differences. Specimens of *fragariae* seem to be less tuberculate; the velvety spots are less distinct and the elytral punctures more widely separated than in specimens of *eubati.* These last mentioned characters may prove to be insignificant when more specimens are examined.

Plant record: Fragaria ananassa (series).

Specimens examined (5 males and 16 females): (Map 13)

UNITED STATES: MAINE: Hancock Co., 8-9 Aug.; Washington Co., 13-20 June. MICHIGAN: Presque Isle Co., 22 Aug. MINNESOTA: Hubbard Co., 3 June, 15 June; Kanabec Co., 27 June; St. Louis Co., 31 May. NEW JERSEY: Middlesex Co., 4 July (?). NEW YORK: Orange Co., 20 July. VERMONT: Windham Co., spring.

CANADA: NEW BRUNSWICK: Kings Co., 17 Sept.; Northumberland Co., 9 July.

Neochlamisus comptoniae (Brown)

Arthrochlamys comptoniae Brown, 1943:125-126.
Atrochlamys charaedapnes Brown; Proctor, 1946:186 (misidentification and misspelling).

Diagnosis: This species is very similar to *cribripennis* except that it is a little larger, punctation on the pygidium and abdominal segments is more uneven, the elytral sculpturing is rougher and the tibial spines in the males are more widely separated. It differs from *assimilis* by the shorter ejaculatory guide and the absence of front tibial spines of the male.

Description: Male: 3.2-3.3 mm long; 2.2-2.4 mm wide. Female: 3.7-4.1 mm long; 2.6-3.0 mm wide. Color dark brownish to reddish bronze; antennae yellowish brown at base, becoming darker brown at apex; frons with small yellow spot in emargination of eye.

Head coarsely punctate on vertex and on lower frons and clypeus; large central depression on upper frons moderately punctate. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum (Fig. 152) coarsely and irregularly striate, with scattered faint punctures, tubercles faint or absent; gibbosity divided, posterolateral slopes regularly striate; posterior lobes transversely, finely striate, impunctate. Mesoscutellum rough, faintly striate, posterior margin flat to slightly depressed, posterolateral corners not reflexed. Elytra (Fig. 151) with small tubercles and carinae, coarsely punctate, punctures usually deep with radiating striae; su-2 broad and rounded, anterior tubercles small and rounded. Pygidium shiny with

smooth medial carina, unevenly punctate, granulate foveae small and faint. Prosternum (Fig. 153) over twice as long as wide. First abdominal segment vermiculate and obscurely foveolate, last segment punctate laterally, mid-ventral surface flat, with two groups of long to short hairs separated by narrow longitudinal smooth area in male; female fovea large, shallow to deep, with scattered lateral hairs. Two well developed spines separated by U-shaped space on front tibia, single similar spine on middle tibia of male; female without tibial spines.

Aedeagus (Fig. 33) broadly pointed, with apex strongly deflexed, large, transparent apical area; ejaculatory guide (Fig. 62) long and robust, length five times width. Spermatheca as in Figure 89.

Type: Male holotype, Natick (Middlesex Co.), Massachusetts, 8 Aug. 1942, on sweet fern, C. A. Frost, no. 5407 in the Canadian National Collection. Male and female paratypes of this species have been examined.

Discussion: This species is closely related to *chamaedaphnes* but differs mainly by having two spines instead of one on the front tibia of the males and more evenly striate posterolateral slopes on the pronotum. Females are extremely difficult to identify because of subjective interpretation of this latter character. It is much easier to identify a series containing both males and females, although males are less frequent in both species. The host plant will be some help in identification, although neither species is restricted to a single host. There is very little difference between *comptoniae* and *assimilis* except for those characters listed in the key. The host plants are different, and *assimilis* has a limited and more southern distribution.

The species referred to by Proctor (1946) as *Atrochlamys charaedapnes* is a misspelling and a misidentification of specimens of *comptoniae*. There are a few specimens of *comptoniae*, including a large series from Cass Co., Minnesota, that have a moderately divided pronotal gibbosity and unevenly striate posterolateral pronotal slopes. In these two respects they resemble *chamaedaphnes*, but in all others, including the two apical spines of the tibia in the males, they are typical *comptoniae*.

A series of 18 specimens labeled "Farmingdale, Florida," are probably mislabeled. The locality does not appear in gazeteers of Florida, and Florida is outside the normal range of the species. There are other specimens collected at Farmingdale, New York, by the same collector at approximately the same date. Four specimens labeled Las Mercedes, California, are considered incorrectly labeled since the locality is so far removed from the known distribution of the species. These localities are not included on the distribution map.

Plant records: Myrica asplenifolia (=Comptonia peregrina) (series with larvae), *Solidago* sp. (series), *Kalmia* sp. (series), and *Corylus* sp. (series).

Specimens examined (66 males and 460 females): (Map 12)

UNITED STATES: CONNECTICUT: Litchfield Co., 23 Mar., 8-14 May, 14-23 June; New Haven Co., 2 Sept.; New London Co., 20 May, 26-28 July, 5-6 Aug.; Tolland Co., 15 May, 6 June. MAINE: Cumberland Co., 1-13 Aug.; Hancock Co., 3 June, July, 12 Sept.; Lincoln Co., 15 June, 5 Aug.; Oxford Co., 8 Sept.; Washington Co., 20 June, 5 July, 16 Aug. MARYLAND: Prince Georges Co., 15 May, 21 July. MASSACHUSETTS: Barnstable Co., 18 Aug., 4 Sept.; Bristol Co., 11 May, 9-14 June, 24 Aug., 6 Sept.; Essex Co., 10 June; Franklin Co., 20 Aug.; Hampden Co., 14 July, 1 Oct.; Middlesex Co., 23 Apr., 6-14 May, 27 May-24 June, 4 July, 22-26 July, 8 Aug.-29 Sept., 10 Oct.; Nantucket Co., Sept.; Norfolk Co., 27 May, June, 1-2 Sept.; Suffolk Co., 20 June, 25 July; Worcester Co., 27 Aug., 14 Sept. MICHIGAN: Gladwin Co., 4 Sept.; Presque Isle Co., 31 July. MINNESOTA: Cass Co., 21-23 Aug.; Hubbard Co., 4 June. NEW HAMPSHIRE: Belknap Co., 3 Aug., 22 Aug.; Carroll Co., 24 June, 19 Aug.; Coos Co., July; Grafton Co., 29 June, 1 Aug.; Hillsboro Co., Sept.; Rockingham Co., no date; Strafford Co., 1 June, 14 Aug. NEW JERSEY: Atlantic Co., 26 May, 12 June, 5 July; Camden Co., 4 May, 30 May, 9 Aug.; Cape May Co., 28 May, 10 June; Monmouth Co., 13-16 June; Ocean Co., 4-9 May, 24-27 May, 17 July, 29 Aug. NEW YORK: Albany Co., 25 Aug.; Clinton Co., 27 June, Essex Co., 1 Sept., 28 Sept., 5 Oct.; Nassau Co., 12 Sept.; Orange Co., 6 July; St. Lawrence Co., 26-27 Aug.; Saratoga Co., 25 Aug.; Suffolk Co., 26 Apr., 28 May, 20 June, 31 July, 25-27 Aug.; Warren Co., 28 Aug.; Wyoming Co., no date. PENNSYLVANIA: Dauphin Co., 6-11 June; Monroe Co., no date; Pike Co., 30 May-June, 17 Sept.; Tioga Co., no date.

Neochlamisus assimilis (Klug)

Chlamys assimilis Klug, 1824:239.
Chlamys affinis Klug, 1824:115-116.
Chlamisus azalae Brown, 1961:972-973 (new synonymy).

Diagnosis: This species is recognized by the presence of a single spine on the front tibia of the female, and the elongate form of the ejaculatory guide.

Description: Male: 3.2 mm long; 2.3 mm wide. Female: 3.5-4.0 mm long; 2.6-3.8 mm wide. Color dark brownish to yellowish bronze; antennae yellowish brown at base, becoming darker brown at apex; frons with small yellow spot in emargination of eye.

Head coarsely punctate on vertex, lower frons and clypeus; large central depression on upper frons faintly punctate. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum coarsely and irregularly striate, finely punctate, tubercles faint or absent; gibbosity slightly divided, posterolateral slopes regularly striate; posterior lobes transversely, finely, carinate; posterior margin depressed, posterolateral corners slightly reflexed. Elytra with small tubercles and carinae, moderately punctate, punctures usually deep with faint radiating striae, su-2 broad and rounded, anterior tubercles small and rounded. Pygidium shiny, with smooth medial carina, coarsely punctate at base, apex becoming finely punctate near middle. Prosternum less than twice as long as wide. First abdominal segment faintly vermiculate and obscurely foveolate; last segment punctate laterally to foveolate near center; mid-ventral surface in male flat, with large group of long and short hairs, female with large shallow fovea and fewer scattered lateral hairs than in male. Two large spines separated by U-shaped

space on front tibia, single similar spine on middle tibia of males; female with single similar spine on anterior and middle tibiae.

Aedeagus (Fig. 34) broadly pointed with apex strongly reflexed; apical area large, transparent; ejaculatory guide (Fig. 63) long and slim, length eight times width, length of basal orifice 1/3 of total length. Spermatheca as in Figure 90.

Type: The Humboldt University Museum, Berlin, has many of Klug's types. There are two female specimens in the collection that are considered by F. Hieke, the curator of Coleoptera, to be the type series. I here designate one of them as lectotype. The type locality is stated as North America. *Chlamisus azaleae:* male holotype, Highlands (Macon Co.), North Carolina, 12 June 1957, W. J. Brown, swept from *Azalea,* no. 6917 in the Canadian National Collection.

Discussion: Female paratypes of *azaleae* agree with the lectotype of *assimilis,* which was borrowed from the Berlin Museum. The only male specimen examined of this species was a male paratype of *azaleae.* Since few specimens were available for study, little is known of variation in the species.

The one specimen from Indiana seems to be out of the range of this species but it is morphologically the same as the other specimens. Additional collecting may indicate a much wider range than is now known for this species.

Plant records: Azalea sp. (series).

Specimens examined (1 male and 8 females): (Map 12)

UNITED STATES: FLORIDA: Jackson Co., 7 Mar.; Osceola Co., no date. INDIANA: Porter Co., 30 July. NORTH CAROLINA: Macon Co., 26-29 June. SOUTH CAROLINA: Oconee Co., no date. VIRGINIA: Fairfax Co., 18 Apr.

Neochlamisus chamaedaphnes (Brown)

Arthrochlamys chamaedaphnes Brown, 1943:130.

Diagnosis: The coarsely striate posterolateral slopes of the pronotum are curved and uneven, the gibbosity is slightly divided, and the elytral tubercles are large. Males have a single spine on the front tibia.

Description: Male: 3.2-3.7 mm long; 2.5-2.7 mm wide. Female: 3.6-4.2 mm long; 2.5-3.0 mm wide. Color dark brown to reddish bronze. Antennae yellowish brown at base, becoming darker brown at apex.

Head finely and faintly punctate, moderately punctate on clypeus and vertex. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum finely punctate, moderately and irregularly striate, tubercles faintly developed; gibbosity moderately divided, posterolateral slopes unevenly striate; posterior lobes transversely, finely striate, impunctate. Mesoscutellum subquadrate, granulate, posterior margin slightly depressed, posterolateral corners reflexed. Elytra (Fig. 154) with large tubercles and

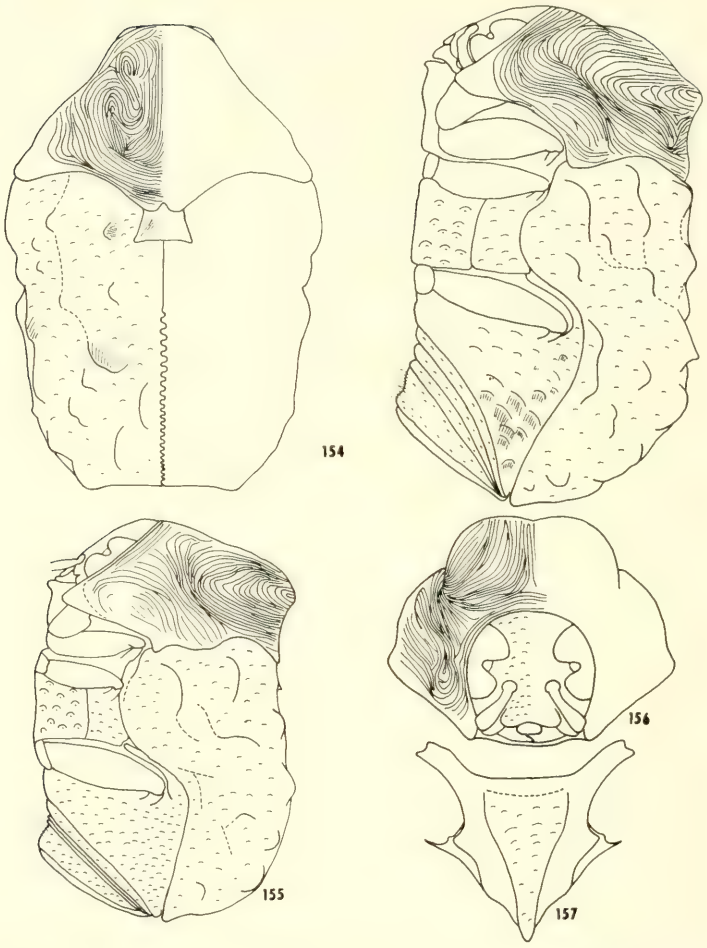


FIG. **154.** *Neochlamisus chamaedaphnes,* dorsal and lateral aspects. FIGS. **155-157.** *Neochlamisus cribripennis.* **155,** dorsal and lateral aspects; **156,** cephalic aspect; **157,** prosternum.

carinae, moderately to coarsely punctate, su-2 broad and rounded; anterior elytral suture closed, posterior 4/5 serrate; anterior tubercles rounded. Pygidium shiny, unevenly moderately to coarsely punctate; foveae shallow and obscure. Prosternum more than 1 1/2 times as long as wide. Abdominal segment partially foveolate, mid-ventral surface of last segment flat with two slightly separated groups of long hairs in male; female with large and deep mid-ventral fovea, lateral hairs more scattered than in male. Single well developed apical spine on front and middle tibiae of male; smaller spines in female.

Aedeagus (Fig. 35) robust, bluntly pointed, with transparent apical

area; ejaculatory guide (Fig. 64) long and robust; length five times width. Spermatheca as in Figure 91.

Types: Male holotype, South March, Ontario, on *Chamaedaphne calyculata,* 19 Sept. 1942, W. J. Brown, no. 5406 in the Canadian National Collection. Allotype and paratypes, same data. I have examined a number of male and female paratypes of this species.

Discussion: The females are sometimes difficult to separate from those of *bebbianae* because of similarities in the pronotum and tibial spines. The posterolateral slopes of the pronotum are more coarsely and irregularly striate in *bebbianae,* and the pronotal gibbosity is more deeply divided. The striations of the pronotum are fairly constant in *chamaedaphnes* and useful in identifying females not associated with males.

Except for *Chamaedaphne calyculata,* all the host plants of this species are shared by many species of the *gibbosus* group. *Corylus americana,* for example, is a host of *platani, bebbianae, eubati, chamaedaphnes,* and probably *comptoniae.* Specimens of *chamaedaphnes* have been taken on *Rubus* sp., *Alnus rugosa, Potentilla fruticosa* and *Vaccinium* sp., all host plants of one or more other species of *Neochlamisus.* It appears that the preferred host of *chamaedaphnes,* as in several other species of this group, may differ in widely separated localities, and that other acceptable hosts occur in each locality.

One specimen labeled Portland, Oregon, is probably mislabeled. It has not been included on the map or in the list of specimens examined.

The reference of Proctor (1946) to *Atrochlamys charaedapnes* in Maine is a misspelling and misidentification. The species referred to is *N. comptoniae.*

Plant records: Potentilla fruticosa (literature record), *Vaccinium* sp. (series), *Alnus rugosus* (series), *Rubus occidentalis* (series), *Chamaedaphne calyculata* (series with larvae), and *Corylus americana* (series).

Specimens examined (59 males and 179 females): (Map 8)

UNITED STATES: CONNECTICUT: Fairfield Co., no date; New Haven Co., 4 Oct. DISTRICT OF COLUMBIA: Washington, 29 July, 30 Sept. KENTUCKY: state record, no date. MARYLAND: Prince Georges Co., 17 Sept. MASSACHUSETTS: Middlesex Co., 18 Apr., 10-13 June, 7-13 Sept., 26-29 Sept., 2 Oct.; Norfolk Co., 15 Aug.; Plymouth Co., 29 May. MICHIGAN: Allegan Co., 17 June; Cheboygen Co., 21 June-3 July, 22 July; Gladwin Co., 4 Sept.; Grand Traverse Co., 27 May; Kent Co., 9 Sept.; Luce Co., 8 Sept.; Marquette Co., 15 June; Schoolcraft Co., 25 Aug.; Van Buren Co., 1 Aug.; Washtenaw Co., 7 July; Wayne Co., Aug. MINNESOTA: Crow Wing Co., 3 July; Hubbard Co., 29 May, 11 Aug.; Lake of the Woods Co., 7 Aug.; Mille Lacs Co., 13-21 May, 3 June; Pine Co., 7 Aug. NEW JERSEY: Burlington Co., 29 June, 12 July; Gloucester Co., 28 June; Hunterdon Co., 30 Apr.; Ocean Co., 25 May, 3 July, 23 Aug. NEW YORK: Chenango Co., 2 Sept.; Genesee Co., 1 July; Herkimer Co., no date; Monroe Co., Oct.; Nassau Co., 12 Sept.; Richmond Co., 1 Oct.; Steuben Co., 20 June; Suffolk Co., 8 May. OHIO: state record, 7 May. VIRGINIA: Arlington Co., 3-5 May, 18 May, 26 June, 20 Sept.; Nelson Co., 26 June; Spotsylvania Co., 21 Mar. WISCONSIN: Oneida Co., 7-8 Sept.

CANADA: ONTARIO: Carleton Co., 20 May, 10 June, 15 Aug., 17-19 Sept.

Neochlamisus cribripennis (LeConte)

Chlamys cribripennis LeConte, 1878:614.
Arthrochlamys cribripennis (LeConte); Brown, 1943:125.
Chlamisus cribripennis (LeConte); Proctor, 1946:186.

Diagnosis: The strongly and evenly punctate pygidium and abdominal segments, together with the subtriangular shape of the prosternum, finely punctate lateral pronotum, and faintly divided pronotal gibbosity, serve to differentiate this species.

Description: Male: 2.8-2.9 mm long; 2.1-2.3 mm wide. Female: 3.3-3.4 mm long; 2.4-2.6 mm wide. Color brownish to reddish bronze; antennae yellowish brown; frons with small yellow spot in emargination of eye.

Head moderately punctate on vertex to coarsely punctate on clypeus. Antennal segment 4 subtriangular, 5 subquadrate, 6-10 rectangular. Pronotum (Fig. 156) coarsely and irregularly striate, lateral areas finely punctate, tubercles faint or absent; gibbosity slightly divided, posterolateral slopes regularly striate, posterior lobes transversely and faintly striate, impunctate. Mesoscutellum granulate, posterior margin flat to slightly depressed, posterolateral corners not reflexed. Elytra (Fig. 155) with rounded, faintly developed tubercles and carinae. Coarsely to moderately punctate, su-2 small but broad; anterior elytral suture closed, posterior 4/5 serrate. Pygidium shiny and moderately to coarsely punctate; no large circular granulated areas. Prosternum (Fig. 157) about twice as long as wide, sides not or only slightly emarginate; posterior process grooved longitudinally. Abdominal segments moderately punctate, almost nonfoveolate; mid-ventral fovea of last segment nearly flat and faintly punctate with scattered hairs, hairs more numerous in male than in female. Two well developed spines on front tibia separated by a V-shaped space, single spine on middle tibia of male; female usually without tibial spines.

Aedeagus (Fig. 36) robust, pointed, with narrow truncate apex; ejaculatory guide (Fig. 65) long and slim, length five times width. Spermatheca as in Figure 92.

Type: Male holotype, collected near Detroit (Wayne Co.), Michigan, in the LeConte collection (MCZ).

Discussion: My specimens of *cribripennis* agree with the holotype except for minor differences. The foveae of the first abdominal segment are less distinct and more confluent in the holotype. Specimens are among the smallest of the *gibbosus* group and also of North American *Neochlamisus*.

There is little variation in the diagnostic characters given, but this may be the result of the availability of too few specimens and the limited number of localities represented. Some specimens of *comptoniae* have the prosternum and pronotal gibbosity similar to those found in *cribripennis*,

although the gibbosity is usually more deeply divided in *comptoniae*. The abdominal segments are also partially punctate in *comptoniae* but never as distinctly, deeply, and uniformly as in *cribripennis*.

Plant records: Vaccinium angustifolium. This plant may not be the only host since only a few specimens were available for study, but it is a host in which large series of both larvae and adults have been observed feeding.

Specimens examined (9 males and 26 females): (Map 13)

UNITED STATES: INDIANA: Porter Co., 22 June. MASSACHUSETTS: Middlesex Co., 19 Sept. MICHIGAN: Cheboygan Co., 11-22 July; Gladwin Co., 4 Sept.; Wayne Co., no date. MINNESOTA: Chisago Co., 16 Aug. WISCONSIN: Douglas Co., 16 Aug.

CANADA: ONTARIO: Carleton Co., 9 June, 10 July, 22-30 July, 6 Sept. QUEBEC: Wright Dist., 28 May; "Duparquet," 2 Aug.; "Peribonca," 24 Aug.

Neochlamisus tuberculatus (Klug)

Chlamys tuberculata Klug, 1824:117-118.
Chlamisus tuberculata (Klug); Fattig, 1948:8.

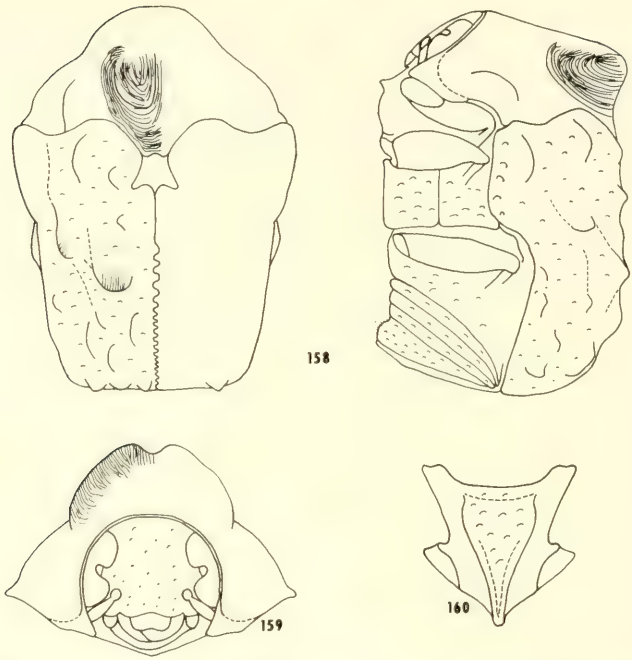
Diagnosis: This small, brightly colored species can be distinguished by the obscurely striate front half of the pronotum, impunctate first abdominal segment, obscurely foveolate pygidium and granulate texture of the elytra.

Description: Male: 2.8-3.0 mm long; 2.1-2.3 mm wide. Female: 2.9-3.3 mm long; 2.2-2.7 mm wide. Color bright brownish to reddish bronze, underside sometimes partially greenish bronze, antennae yellow to light brown.

Head finely punctate, except more coarsely punctate on clypeus and vertex. Antennal segment 4 subtriangular, 5 subrectangular, 6-10 rectangular. Pronotum (Fig. 159) faintly, finely, and irregularly striate, tubercles faintly developed; gibbosity moderately or slightly divided, posterolateral slopes moderately and regularly striate; posterior lobes transversely, finely striate, impunctate. Mesoscutellum subquadrate, granulate, posterior margin slightly depressed. Elytra (Fig. 158) with small tubercles and carinae, finely punctate; several deep punctures on disc in some specimens; anterior elytral suture closed, posterior 4/5 serrate. Pygidium with faint medial carina, centrally foveolate; small shallow fovea becoming convergent and obscure laterally. Prosternum (Fig. 160) subtriangular, about twice as long as wide; sides only slightly emarginate. First abdominal segment obscurely foveolate, impunctate; last abdominal segment with many small foveae laterally, mid-ventral area flat with two groups of hairs in male; female with slightly depressed large fovea with scattered hairs laterally. Two well developed tibial spines, separated by U-shaped space, on front tibia, single similar spine on middle tibia; female tibiae without spines.

Aedeagus (Fig. 37) robust with acute apex; ejaculatory guide (Fig. 66) long and slim. Spermatheca as in Figure 93.

Types: The type of *tuberculatus* is supposed to be in the Humboldt University Museum, Berlin, but was not located there. I assume, from the



FIGS. **158-160.** *Neochlamisus tuberculatus.* **158,** dorsal and lateral aspects; **159,** cephalic aspect; **160,** prosternum.

descriptions by Klug and Lacordaire, as well as the type locality, that I have correctly identified the species. Its small size and sculpturing make this one of the more easily recognized species of the *gibbosus* group.

Discussion: This species has many similarities to *cribripennis* but the two are easily distinguished by the characters given in the key. They also are quite distinct geographically and can be separated by means of locality. Both are somewhat restricted in distribution as compared to most of the other species in this group. Most of the specimens examined show little variation in the usually variable characters mentioned for the group. A few specimens, however, are more tuberculate and striate than usual and have moderately deep punctures in the region of the elytra where some species have a small velvety spot. The other elytral punctures are also larger and more depressed. Other characters in these individuals agree with those of *tuberculatus* so I am placing them in this species.

Plant records: Vaccinium sp. and *Quercus* sp.

Specimens examined (42 males and 48 females): (Map 13)

UNITED STATES: ALABAMA: Tallapoosa Co., Aug. ARKANSAS: Benton Co., 6 June. FLORIDA: Alachua Co., 13 Mar., 19 Apr.-6 May, 21-31 May; Brevard Co., 8 Nov.; Duval Co., no date; Hamilton Co., 6 June; Hendry Co., 26 Feb., 20 Apr.; Highlands Co., 5 May, 16 June; Hillsborough Co., 13 Apr.-7 May; Lee Co., 23 Apr., 3-5 May; Levy Co., 4 Apr., 17 July;

Okeechobee Co., 28 Feb.; Osceola Co., 19 Feb.; Pasco Co., 13 July; Pinellas Co., 20 Jan., 9-11 Feb., 21 Mar., 2 Apr., 29-30 Apr., 14 Nov., 26 Nov., 15 Dec., 30 Dec.; Seminole Co., 5 Apr., May; Suwannee Co., 3 July; Volusia Co., 10-15 Apr., 25 May, 5 Oct. GEORGIA: Charlton Co., June-25 July; Clarke Co., 2 May; Union Co., 25 May. INDIANA: Harrison Co., 26 Sept. MARYLAND: Anne Arundel Co., 21 May. NORTH CAROLINA: Harnett Co., no date; New Hanover Co., no date. SOUTH CAROLINA: Kershaw Co., 29 May.

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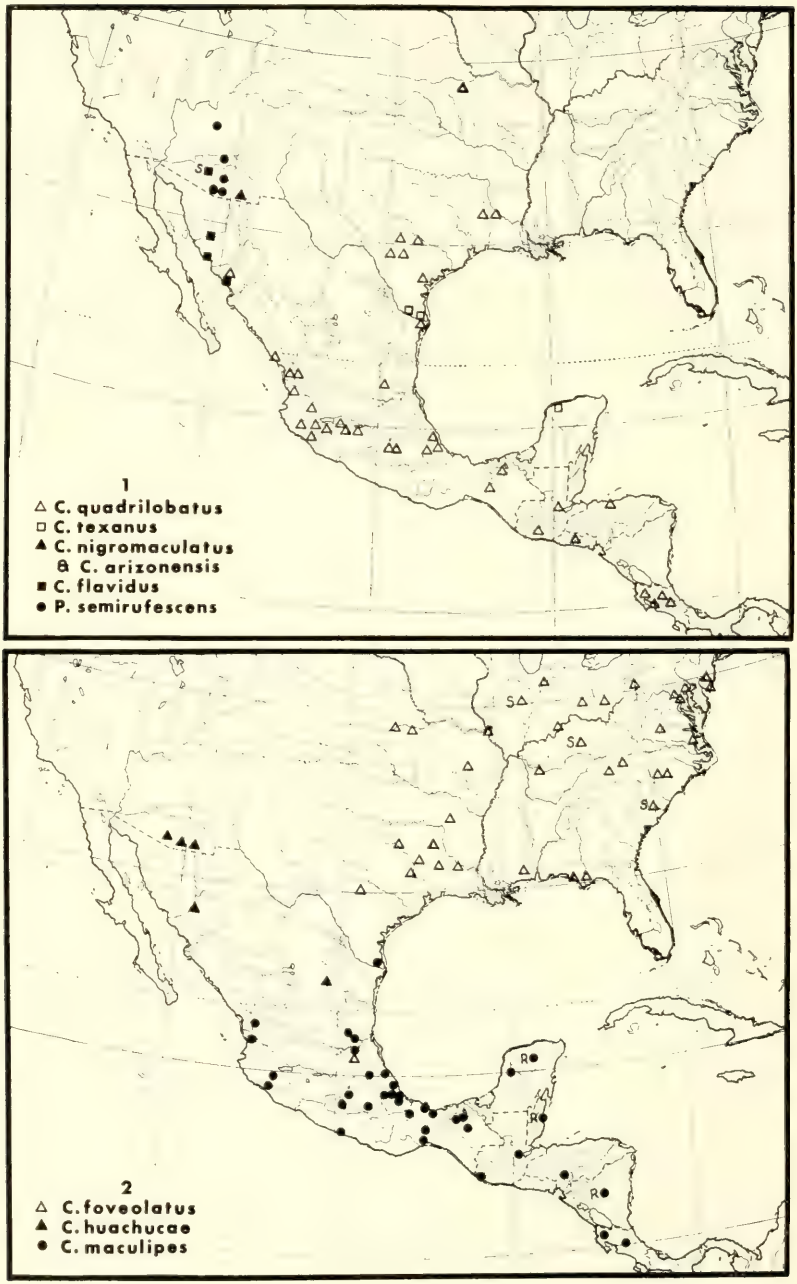
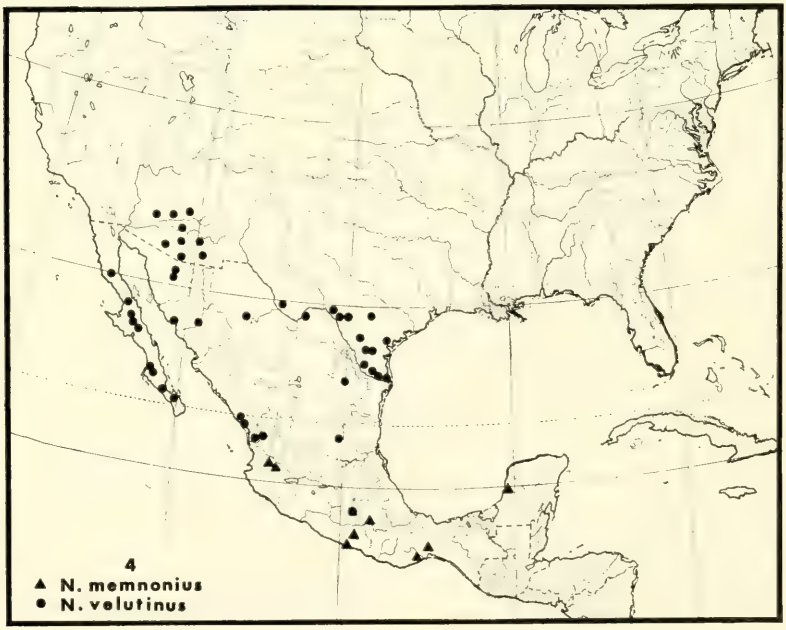
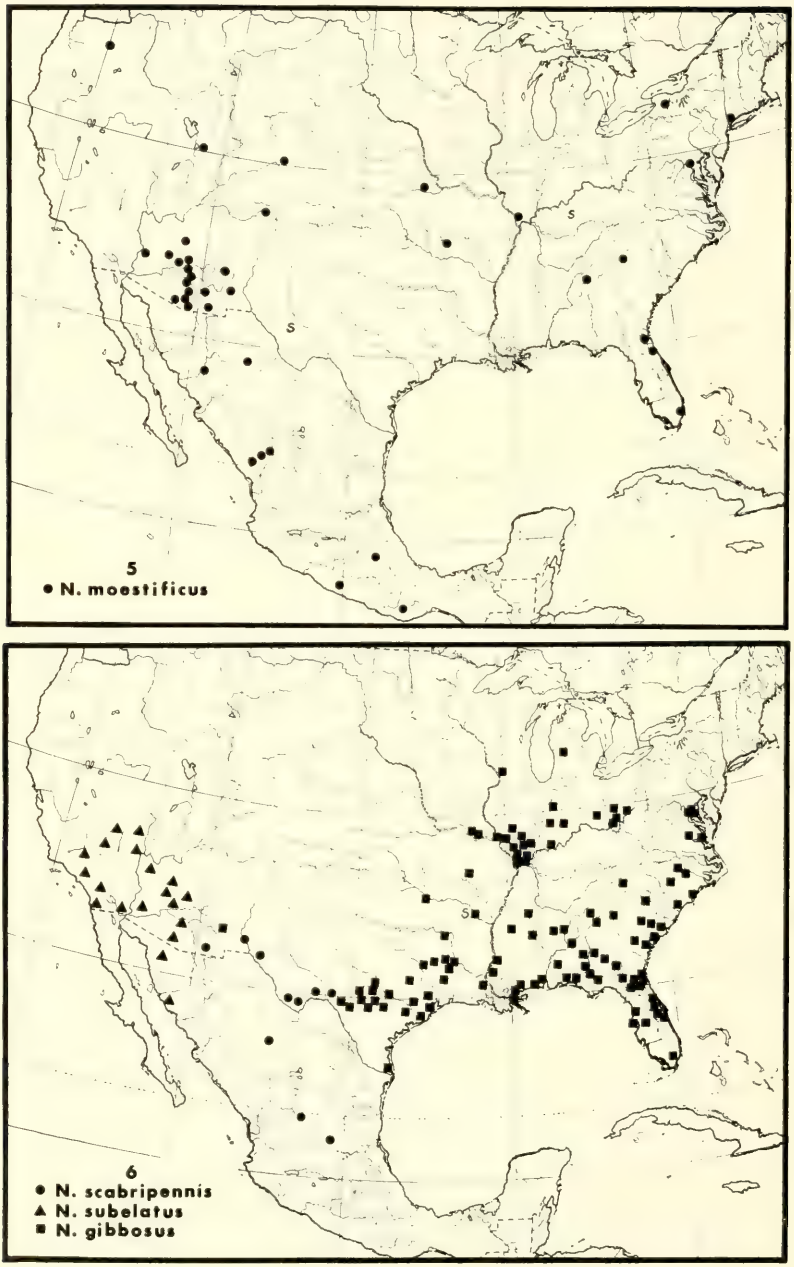


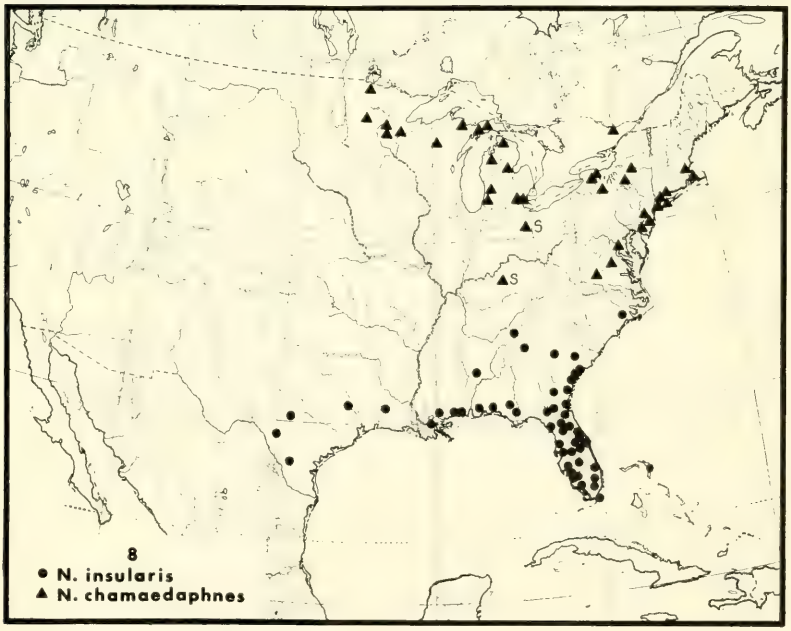
MAP 1. Range of *Pseudochlamys semirufescens, Chlamisus flavidus, C. arizonensis, C. nigromaculatus, C. texanus,* and *C. quadrilobatus.* MAP 2. Range of *Chlamisus foveolatus, C. huachucae,* and *C. maculipes.* Each spot represents one or more collections within a county or at a locality. S=state record. R=indefinite locality within a country.



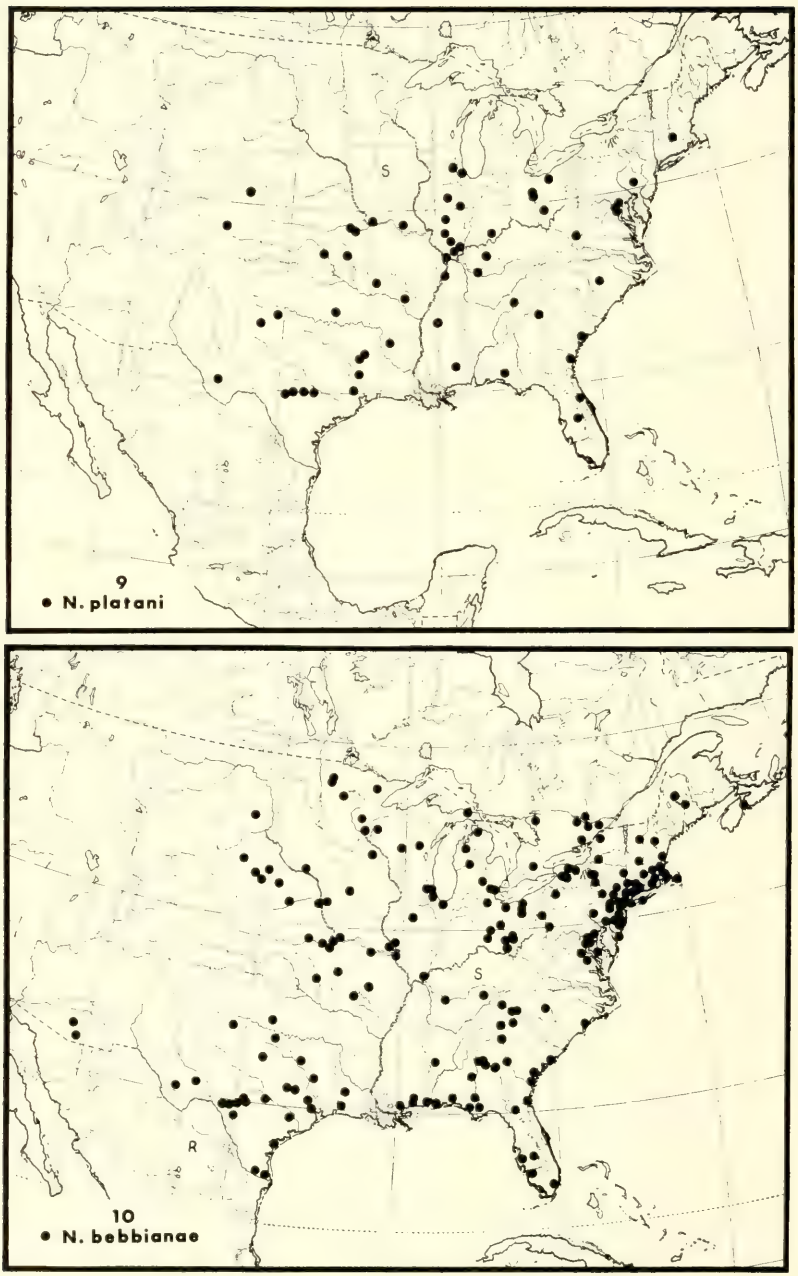
Map 3. Range of *Diplacaspis prosternalis*. Map 4. Range of *Neochlamisus velutinus* and *N. memnonius*. Each spot represents one or more collections within a county or at a locality.



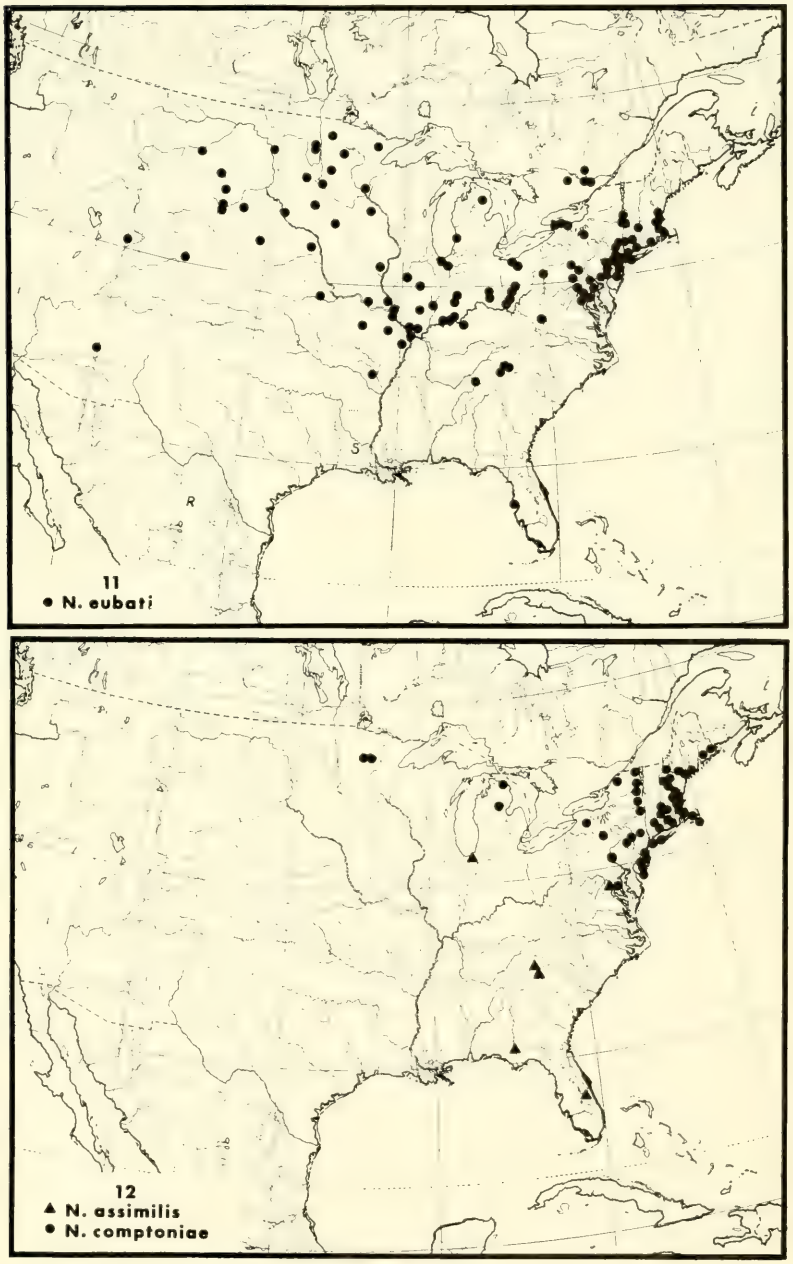
MAP 5. Range of *Neochlamisus moestificus*. MAP 6. Range of *Neochlamisus scabripennis*, *N. subelatus*, and *N. gibbosus*. Each spot represents one or more collections within a county or at a locality. S=state record.



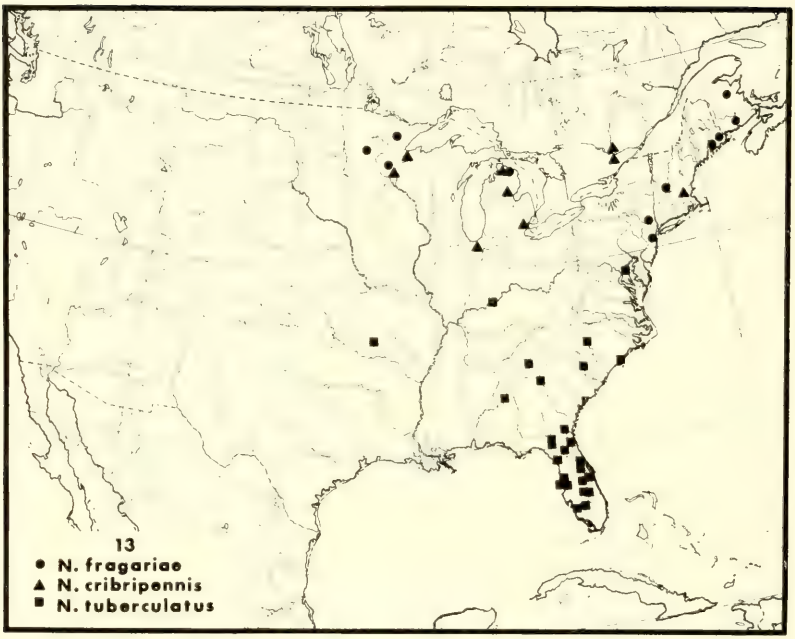
Map 7. Range of *Neochlamisus bimaculatus*. Map 8. Range of *Neochlamisus chamaedaphnes*, and *N. insularis*. Each spot represents one or more collections within a county or at a locality. S=state record.



MAP 9. Range of *Neochlamisus platani*. MAP 10. Range of *Neochlamisus bebbianae*. Each spot represents one or more collections within a county or at a locality. S=state record. R=indefinite locality record within a country.



Map 11. Range of *Neochlamisus eubati*. Map 12. Range of *Neochlamisus comptoniae* and *N. assimilis*. Each spot represents one or more collections within a county or at a locality. S=state record. R=indefinite locality within a country.



MAP 13. Range of *Neochlamisus fragariae*, *N. cribripennis*, and *N. tuberculatus*. Each spot represents one or more collections within a county or at a locality.

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